WINTER AND SPRING MIGRATION ECOLOGY OF BLACK BRANT *(BRANTA BERNICLA NIGRICANS)* IN THE STRAIT OF GEORGIA, BRITISH COLUMBIA

Katherine Hagmeier

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ABSTRACT

A population may be defined as a group of organisms living in a particular space at a particular time. Understanding processes that affect population change is essential for conservation and management of many populations, but depends on the spatial and temporal scale within which the population is examined. The Pacific Flyway Brant Population in North America contains both winter resident and spring transient populations at different times in an annual cycle. Furthermore, there are two distinct taxa within the Flyway population: Black Brant (*Branta bernicla nigricans*) which comprise >90% of the Flyway population and Grey-bellied Brant, one of four distinct stocks of Light-bellied Brant (*Branta bernicla hrota*), which comprise the remainder of the population.

A small population of Brant winters in the Boundary Bay and Roberts Bank area of the Fraser River delta in southern British Columbia, Canada. This population has increased rapidly since the 1990's due to a combination of annual productivity and immigration. The largest source of immigration is from Grey-bellied Brant, which traditionally winter in northern Washington State, USA, 60 km south of the Fraser River delta. Increased integrated management of the Boundary Bay-Roberts Bank wintering Brant and Brant wintering in Washington State is recommended. Wintering Brant in Boundary Bay and Roberts Bank are subjected to high levels of disturbance. The frequency of disturbance was 2.17/h in Boundary Bay and 1.32/h in Roberts Bank. Brant spent approximately 10% of their time responding to disturbance and this amounted to an estimated 45% of their daily energy expenditure. There is potential for wintering Brant to abandon the area if the levels of disturbance remain high or increase. The most common source of disturbance was Bald Eagles, hence reducing disturbance will be challenging for managers.

During spring migration, transient populations of Brant stage in two key areas in the Strait of Georgia, British Columbia. These are Boundary Bay and Roberts Bank and Parksville-Qualicum on the east coast of Vancouver Island, British Columbia. To estimate the total number of Brant using these two areas, weekly counts combined with capture-mark-recapture analysis using Program Mark were used to develop models describing spring migration patterns. These models revealed that the areas support largely separate migrating populations. Results also revealed that between 13-27% of the Pacific Flyway Brant Population staged in Boundary Bay and Roberts Bank and Parksville-Qualicum in 1999 and 2000. Conservation of

these two staging areas may be critical for the successful management of the Pacific Flyway Brant Population.

RÉSUMÉ

On peut définir une population comme un groupe d'organismes qui vivent en un espace et une période donnés. La connaissance des processus qui déterminent les changements démographiques est essentielle pour la conservation et la gestion de nombreuses populations, mais il faut garder à l'esprit que cette connaissance est fonction des échelles spatiale et temporelle à l'intérieur desquelles nous étudions les populations. La population de Bernaches cravants de la voie migratoire du Pacifique de l'Amérique du Nord comprend des populations hivernantes et des populations migratrices qu'on trouve en divers endroits à différentes périodes du cycle annuel. De plus, on compte deux taxons distincts dans la population de cette voie migratoire : la Bernache cravant noire (*Branta bernicla nigricans*), qui représente plus de 90 % de la population, et la Bernache cravant à ventre gris - l'une des quatre formes de la Bernache cravant à ventre pâle (*Branta bernicla hrota*) -, qui constitue le reste de la population. Une petite population de Bernaches cravants hivernent dans la région de la baie Boundary et du banc Roberts, dans le delta du Fraser, en Colombie-Britannique (Canada). Cette population s'est rapidement accrue depuis les années 1990, grâce à une bonne productivité annuelle et à l'immigration. Les immigrants sont surtout des Bernaches cravants à ventre gris, forme qui a l'habitude d'hiverner dans le nord de l'État de Washington (États-Unis) à 60 km au sud du delta du Fraser. On recommande donc une gestion intégrée accrue des bernaches hivernantes du secteur baie Boundary-banc Roberts et du Washington.

Les Bernaches cravants qui hivernent dans la région de la baie Boundary et du banc Roberts sont exposées à de forts niveaux de perturbation. On a observé des fréquences de perturbation de 2,17/h à la baie Boundary et de 1,32/h au banc Roberts. Les bernaches passaient environ 10 % de leur temps à réagir aux perturbations, ce qui, selon nos estimations, requérait une quantité d'énergie correspondant à 45 % de leurs dépenses énergétiques quotidiennes. Il est possible que les bernaches cessent d'hiverner à cet endroit si les niveaux de perturbation demeurent élevés ou s'accroissent. La principale source de perturbation observée étant les Pygargues à tête blanche, la réduction des niveaux de perturbation représentera un défi de taille pour les gestionnaires.

Durant la migration printanière, les bernaches de passage font halte dans deux secteurs clés dans le détroit de Géorgie (Colombie-Britannique), soit celui de la baie-Boundary et du banc Roberts, et celui de Parksville-Qualicum sur la côte est de l'île de Vancouver (Colombie-Britannique). Pour estimer le nombre total de bernaches présentes à ces deux

endroits, on a effectué des dénombrements hebdomadaires et une analyse de données de marquage-recapture au moyen du programme Mark en vue d'élaborer des modèles décrivant les profils de migration printanière. Les modèles obtenus ont montré que ces deux régions sont fréquentées par des populations migratrices largement distinctes. Les résultats ont aussi montré que de 13 à 27 % de la population de Bernaches cravants de la voie migratoire du Pacifique a fait halte dans les secteurs baie Boundary-banc Roberts et Parksville-Qualicum en 1999 et 2000. La conservation de ces deux haltes migratoires pourrait s'avérer essentielle pour assurer le succès de la gestion de la population de Bernaches cravants de la voie migratoire du Pacifique.

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1. GENERAL INTRODUCTION

1.1 Population Dynamics

A population may be defined as a group of organisms of the same species living in a particular space at a particular time (Krebs 1985). This definition necessarily changes depending on the spatial scale being examined and is also complicated by the fact that a population may be divided into distinct components, which may have behavioural, morphological or geographical differences.

Population size is primarily regulated by four factors: 1) natality, 2) mortality, 3) immigration and 4) emigration (Begon *et al.* 1990). Ultimately, each of these is a response to limiting factors in the environment (e.g. availability of food and water, or nest sites). Accordingly, an over-abundance of a limiting resource leads to an increase in population size. If there are no limiting factors, growth will remain unchecked so that a population experiences exponential growth (Johnson 1994). However, in most natural systems, the growth rate declines once a balance is achieved between the population and its environment (i.e. the carrying capacity). Understanding this balance is particularly critical when humans influence the environment through habitat loss or degradation.

Within a population, differences in migration patterns and annual life history strategies likely develop from trade-offs made by individuals in order to maximize fitness (Cox 1968, Gauthreaux 1982, Cox 1985). Migration patterns are commonly associated with bird species, particularly Arctic-nesting waterfowl and shorebirds, many of which have evolved highly specialized strategies (Raveling 1979, Gauthreaux 1980, Owen and Black 1990). Differences in migration strategies within a population may complicate the calculation of estimates of that population in temporary, but critical staging areas. Yet, estimates of migratory populations are essential as the importance of spring and fall staging habitats is often measured by the volumes of birds using the sites (Thompson 1993, Routledge *et al.* 1999, Frederickson *et al.* 2001).

In this study I investigated the population demography of Arctic-nesting Brant Geese (*Branta bernicla*), both wintering and migrating, in the Strait of Georgia, British Columbia. In doing so, I identified different segments of the Pacific Flyway Brant Population and described their interactions with the environment.

1.2 Study Species: Brant (*Branta bernicla*)

Brant (*Branta bernicla*) is a small sea goose that breeds in the North American and Eurasian Arctic. In North America, Brant are classified into two subspecies, the light-bellied *Branta*

bernicla hrota and the Black Brant, *Branta bernicla nigricans* (Madsen *et al.* 1999). *B. b. hrota* is further subdivided into two distinct stocks, Atlantic Brant and Grey-bellied Brant, which should be considered as separate taxa in terms of conservation and management (Madsen *et al.* 1999). The taxa are genetically, morphologically, and geographically distinct (Shields 1990). The number of Grey-bellied Brant is estimated between 6000-9000 birds (Subcommittee on Pacific Brant 2001) and is therefore one of the smallest Arctic goose stocks in the world (Brewer *et al.* 1999).

The Pacific Flyway Brant Population contains Black Brant and Grey-bellied Brant. Together, between 120,000-150,000 Brant migrate along the Pacific Flyway each year (Subcommittee on Pacific Brant 2001). Grey-bellied Brant breed exclusively in the Canadian High Arctic on Melville, Prince Patrick and Eglington Islands and winter in a discrete area in northern Washington State (Padilla, Fidalgo and Samish Bays) (Reed *et al.* 1989, Sedinger *et al.* 1994). Black Brant have a broader breeding range, the largest colonies of which are on the Yukon-Kuskokwim (Y-K) Delta in southwestern Alaska. Ninety percent of the Black Brant winter in Mexico (approximately 75% of the entire Pacific Flyway Brant Population). The remaining birds winter as small units along the Pacific Coast between Alaska and California (Figure 1) (Sedinger *et al.* 1994). Throughout this thesis, I will refer to Black Brant and Grey-bellied Brant together as Brant unless I make a distinction.

1.3 Population Structure

The Pacific Flyway Brant Population is regulated by factors that influence mortality and recruitment. It is widely accepted that harvest mortality is additive to natural mortality and, particularly in years when there has been low productivity combined with high harvest, harvest mortality negatively influences population size (Ebbinge 1991, Sedinger *et al.* 1994, Madsen *et al.* 1999). The structure of the Pacific Flyway Brant Population can be divided into three parts: 1) 30% are successful breeding adults, 2) between 16-28% are young, and 3) the remainder, non-breeders or failed breeders (Sedinger *et al.* 1994). Changes in the non-breeding portion do not affect the population as severely as changes in successful breeders; however, non-breeders may act as a buffer, which add to the breeding population over time to compensate for periods of low recruitment. Brant develop long-term, pair bonds and both members of the pair are involved in parental care. Family units migrate together during the year, although their family cohesiveness is not as easily detected as in other species of Arctic-nesting geese (Reed 1993).

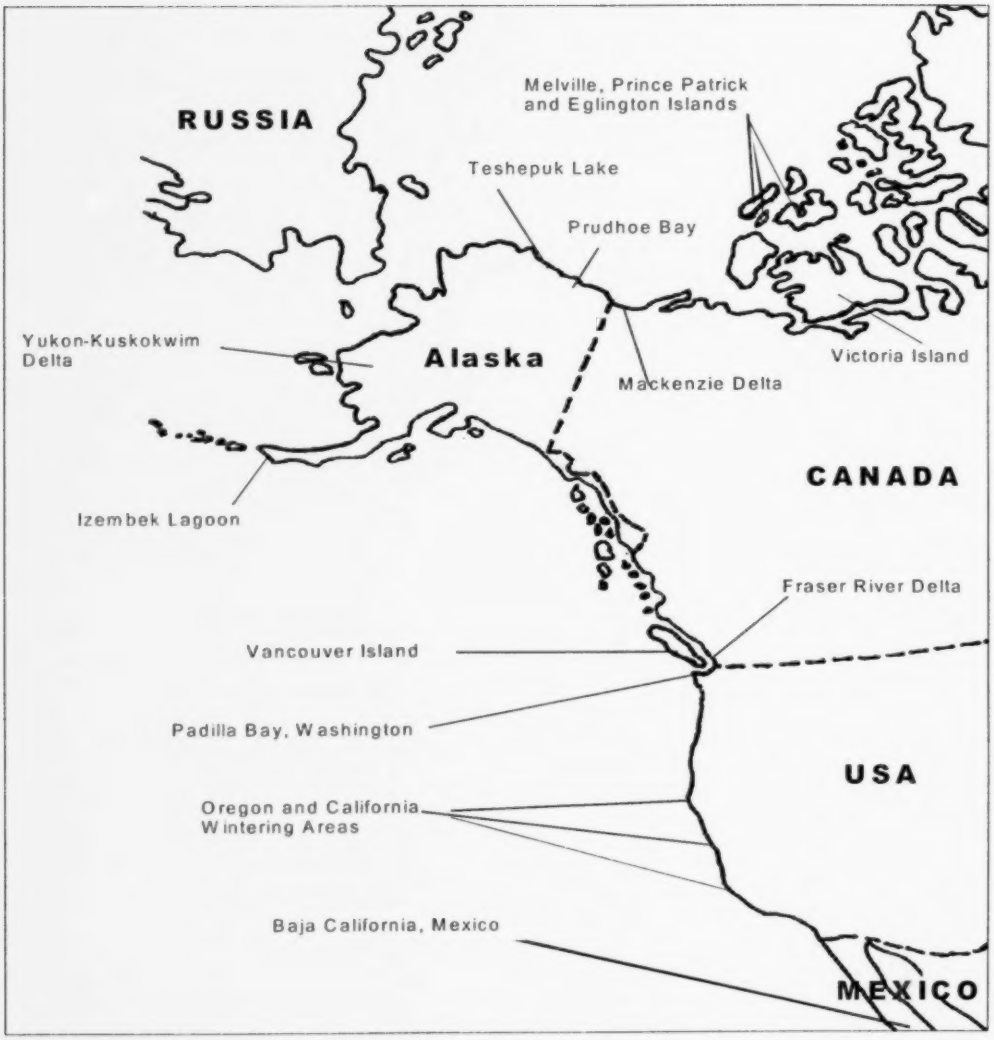


Figure 1. Important breeding, wintering and spring staging areas of the Pacific Flyway Brant Population.

1.4 Habitat

The primary food of Brant is eelgrass (*Zostera* species) (Cottam *et al.* 1944, Einarsen 1965, Charman 1977, Ganter 2000), but other foods include algae (*Ulva* spp and *Enteromorpha* spp) and roe deposited by Pacific Herring (*Clupea harengus*) (Nygren 1990). Brant also ingest grit and regularly haul out on sandy beaches and spits (Campbell *et al.* 1990).

In winter Brant use sheltered coastal areas, typically estuaries, beaches, bays, lagoons and mudflats (Campbell *et al.* 1990). One of the greatest threats to Brant is the loss of wintering habitat (Sedinger *et al.* 1994). Development, driven by urbanization in temperate, coastal areas has caused increased disturbance to Brant and the deterioration or complete loss of habitat (Sedinger *et al.* 1994).

During migration, Brant stage in areas with abundant eelgrass. The most important of these staging areas is Izembek Lagoon on the tip of the Alaskan Peninsula (Figure 1). This is the final staging ground before Brant depart to the breeding grounds and is again important during autumn migration (Dau 1992).

The Y-K Delta contains the largest colonies of nesting Brant. In years when the area is covered in snow when the Brant arrive, they must delay nesting until conditions are suitable. Therefore, females must rely on stored nutrients acquired during migration when waiting to initiate nesting and they utilize these endogenous reserves during incubation. In late years fewer and smaller clutches occur (Sedinger *et al.* 1994).

1.5 Study Area

Research was conducted in the Strait of Georgia, British Columbia (Figure 1). During the winter (November to February), research was focused in Boundary Bay and Roberts Bank on the Fraser River delta (Figure 2). During the spring (March-May) the study area was expanded to include the east coast of Vancouver Island between Campbell River and Parksville. This allowed for observation of migrating Brant staging in two key areas as they moved north to the breeding grounds. Effort on Vancouver Island was concentrated on the main staging area between Parksville and Qualicum.

1.6 Study Objectives

I had two major goals in this study. The first was to understand the population dynamics of Brant wintering in Boundary Bay and Roberts Bank. This includes distribution, abundance, population composition, activity budgets, and examination of the current harvest regime. The second goal was to develop a model that will facilitate estimates of the number of Brant staging in Parksville-Qualicum and the Fraser River delta during spring migration.

Figure 2. Brant staging areas along the Strait of Georgia.

2. BRANT WINTERING IN BOUNDARY BAY AND ROBERTS BANK, BRITISH COLUMBIA: POPULATION DYNAMICS

2.1 Introduction

The global Brant population is comprised of three subspecies, Black Brant (*Branta bernicla nigricans*), Dark-bellied Brant (*B. b. bernicla*) and Light-bellied Brant (*B. b. hrota*). Dark-bellied Brant are found in Europe, Black Brant are found in North America and Light-bellied Brant are a combination of four stocks, which should be considered separately for conservation purposes (Madsen *et al.* 1999). Two of the Light-bellied stocks winter in Europe (the Eastern Canadian High Arctic Light-bellied Brent and the Svalbard Brent) and two winter in North America (the Atlantic Brant and the Grey-bellied Brant). In North America, the Light-bellied Atlantic Brant breed in the Eastern Canadian High Arctic and winter along the Atlantic Coast of the United States from Massachusetts to South Carolina. The other North American Light-bellied stock is the Grey-bellied Brant which breed on Melville, Prince Patrick and Eglington Islands in the Western Canadian High Arctic and winter along the northern coast of Washington State (Figure 1).

The Pacific Flyway Brant Population is comprised of Black Brant and Grey-bellied Brant (Reed *et al.* 1989, Shields 1990, Reed 1997). The two taxa have geographical, morphological and genetic differences (Shields 1990). Black Brant occur as an aggregate of smaller wintering populations. The majority (~75%) winter on the Baja California peninsula and the west coast of Mexico (Sedinger *et al.* 1994). The rest winter as small units in sheltered bays and estuaries between Alaska and California. Unlike Black Brant, Grey-bellied Brant have a small winter range concentrated on Samish, Fidalgo and Padilla Bays in Washington State (Reed *et al.* 1989) and comprise less than 10% of the total Pacific Flyway Brant Population (Brewer *et al.* 1999).

Historically in British Columbia, a wintering population of Black Brant appeared in late autumn in Boundary Bay on the Fraser River delta. In addition, from approximately March until May, Brant migrating from more southern wintering areas (Washington, California, Oregon and Mexico) formed a transient spring population in Boundary Bay that intermingled with the wintering birds. By late May, all Brant had departed. However, Brant abundance has changed considerably in British Columbia during the last century. Records show that Brant were abundant winter residents in Boundary Bay in the late 1800's (Fannin 1891), but were considered primarily spring transients by the 1940's (Campbell *et al.* 1990). Ladner Christmas Bird Counts show declines in wintering Brant, e.g., 600 birds in 1960, 83 in 1962, and zero in 1980 (Campbell *et al.* 1990). The overall decline has been attributed to disturbance and over-hunting (Leach 1979).

Declines occurred elsewhere in the Pacific Flyway Brant Population, reaching historic lows in the 1970's and 1980's (Sedinger *et al.* 1994). This prompted changes in the British Columbia Brant harvest regulations. In 1977 hunting was restricted to the first 10 days of March on the Fraser River delta, was permanently closed on Vancouver Island in 1979, and also on the Queen Charlotte Islands in 1984 (BC Ministry of Environment, Lands and Parks unpubl. data.). The spring hunting season on the Fraser River delta was modified to concentrate the harvest on transient spring migrants. The impact of the British Columbia hunting season, however, remains a management concern. Variation in the timing of migration influences the number of spring migrants present on the Fraser River delta before and during the hunt. Furthermore, the harvest of spring migrants may adversely affect the recovery of other small wintering units on the Pacific Flyway.

By 2000, the number of Brant wintering in Boundary Bay increased to approximately 1200 birds (unpubl. data). Brant also expanded their winter range to include Roberts Bank, west of

Boundary Bay, an area not historically used by wintering Brant. The greatest changes in abundance and distribution occurred in the late 1990's (Reed 1997, unpubl. data), but the specific mechanisms for these rapid changes are not well understood.

In recent years, large numbers of Grey-bellied Brant (~200 or 18%) have been observed wintering in Boundary Bay and Roberts Bank. This is likely a new phenomenon as there are no historical references of Grey-bellied Brant wintering in Boundary Bay. According to local hunters, a Grey-bellied Brant shot during the hunting season in the 1980's and early 1990's was a rare event (Garry Grigg pers. comm.). In 1994-95 and 1995-96 estimates of Grey-bellied Brant in the Boundary Bay wintering population were 3.0% (± 2.6 SD) and 5.3% (± 2.5 SD) respectively (Reed unpubl. data).

Adequate monitoring of Brant and understanding the factors influencing population change are essential for the conservation of the Boundary Bay-Roberts Bank wintering population. In addition, identifying the impacts of the spring hunt could have management implications that extend to other wintering units on the Pacific Flyway. Therefore, this chapter examines population demographics of Brant in Boundary Bay and Roberts Bank. Specific objectives were to estimate the annual numbers of Brant wintering in Boundary Bay and Roberts Bank, identify the population composition in terms of annual productivity, breeding ground origin, and the proportion of Grey-bellied Brant, compare daily use of Boundary Bay and Roberts Bank, and determine the impact of hunting.

2.2 Methods

2.2.1 Study area

In Boundary Bay and Roberts Bank, Brant forage on eelgrass and haul out on spits. In 1989, 55% (2839 ha) of Boundary Bay was covered with eelgrass (*Zostera marina* and *Zostera japonica*) (Ward *et al.* 1992) and the eelgrass beds have continued to increase (Tarbotton and Harrison 1996). The sandy spit at Beach Grove is used for loafing, preening, and gritting (Reed 1997). During the time frame of this study, wintering Brant expanded their range to include Roberts Bank (pers. obs.). Between 1959 and 1994 the surface area of Roberts Bank covered with eelgrass increased from 395 to 700 ha (Tarbotton and Harrison 1996). Boundary Bay and Roberts Bank are both areas of high recreational activity and support the only Brant hunt in British Columbia.

2.2.2 Data Collection

Researchers examining breeding and migratory patterns of the Pacific Flyway Brant Population have marked Black Brant on the breeding and moulting grounds with coded, coloured leg-bands since 1985 (Bollinger unpubl. data). As a result, 8-10% of Black Brant in the Pacific Flyway Brant Population are individually marked (Reed 1997). Leg-banded Brant can be observed on winter and migratory staging areas and I capitalized on this during my research. During my research Grey-bellied Brant did not carry leg-bands.

During the winters and springs of 1997-98, 1998-99, and 1999-2000 Brant were surveyed daily in Boundary Bay and Roberts Bank. Each year surveys began when Brant arrived from the breeding grounds (approximately November) and lasted until spring migration (approximately May). Each survey was conducted with a 20-60X spotting scope to record leg-band data and conduct counts. Leg-band data were collected in order to identify winter residents of Boundary Bay and Roberts Bank and their breeding ground affiliations. Leg-band data were also used to identify when Brant from more southern wintering areas arrived in Boundary Bay and Roberts Bank.

Each day, the maximum number of Brant was recorded at each site. Concurrent counts of both sites were conducted 2-3/week to estimate the total number of Brant in the study area. I examined population composition by scanning groups of Brant (usually ~100 birds) and counting the number of each taxon, the number of banded birds (recording colour and code), and the number of immature Black Brant. Immature Brant were distinguished by the presence of white on the edges of their wing coverts and secondary feathers. Surveys for immature Grey-bellied Brant were added in the final year of the study.

Grey-bellied Brant were distinguished from Black Brant by belly plumage. This difference was observed when the birds were standing out of the water. The black plumage is continuous from the neck to the lower abdomen on Black Brant, whereas there is a sharp contrast between the black breast and the pale abdomen on Grey-bellied Brant. Because of plumage variability (i.e. some Grey-bellied Brant appear dark and cannot be easily differentiated from Black Brant) the estimates of Grey-bellied Brant in this research are minimum estimates. During subsequent research, I have learned that the necklace is a reliable feature for differentiating Black and Grey-bellied Brant (see Boyd and Maltby, 1979).

2.2.3 Analysis

Abundance

In this study, the wintering Brant population was defined as those birds present between December 15 and January 31. This definition was likely conservative as the wintering population appeared to have formed by the end of November and spring migrants did not appear to arrive until mid-February (Reed 1997, pers. obs). Fall migrants seem to be absent in Boundary Bay and Roberts Bank (Reed 1997). To estimate the annual abundance of the wintering population, I used maximum and mean counts observed between December 15 and January 31 each year.

I also estimated Brant goose-day use for each winter (where a goose day is defined as the presence of one goose for one day). To calculate cumulative goose-days I used the formula:

$$\text{Goose-days} = \sum_i \frac{N_i (D_{i+1} - D_{i-1})}{2} \qquad \text{(Equation 1)}$$

where N_i = population at i^{th} survey, D_i = date of i^{th} survey, D_{i+1} = next survey date, D_{i-1} = previous survey date. By definition, $D_0 = D_1$ and $D_{n+1} = D_n$ (Boyd 1995).

Population Composition and Increase

Like all populations, the wintering Brant population is influenced by four factors: immigration, emigration, annual productivity and mortality (Begon *et al.* 1990). Accordingly, when population increase cannot be accounted for by annual productivity and mortality, the balance must be from immigration. To determine if annual productivity and/or immigration were responsible for the rapid growth in the population, I examined population composition.

To estimate population composition, the numbers of immature Black Brant, Grey-bellied Brant, and Brant from each breeding ground were converted to proportions of the population using the Jackknife technique (Cochran 1977). The proportions of immature Black Brant in the population (i.e. annual productivity) and Grey-bellied Brant were examined to determine how each group contributed to annual increases in the population. I used the equations:

$$N_{y+1} = N_y - M_y + (I_{y+1}) \qquad \text{(Equation 2a)}$$

$$N_{y+1} = N_y - M_y + (G_{y+1}) \qquad \text{(Equation 2b)}$$

$$N_{y+1} = N_y - M_y + (I_{y+1} + G_{y+1}) \qquad \text{(Equation 2c)}$$

where N = total number of wintering Brant, y = year, M = number of mortalities, I = number of immature Black Brant and G = the number of Grey-bellied Brant.

I calculated this set of equations for each index of abundance and compared the results with the observed values to determine which equation best predicted population growth. The estimates of immature Black Brant and Grey-bellied Brant were obtained from the survey data. Mortality consisted of two components, natural and hunting mortality. I assumed a 6% annual natural mortality as observed in other Brant and goose populations (Ebbinge 1991). Hunting mortality is estimated under the harvest section of this chapter.

I also modeled population increase using exponential growth equations. The models were designed to show the level of annual productivity necessary to account for the annual increases in the population. I modeled maximum and mean count data that were available between 1993-94 and 1999-2000. I compared the results with the observed annual productivity to see if the values generated by the models were supported by the data. An exponential model is based on continuous growth so the instantaneous rate of increase was modified to provide an estimate of annual productivity based on discrete growth (Caughley and Birch 1971) as Brant have one reproductive season each year:

$$r_d = e^{rt} - 1 \qquad \text{(Equation 3)}$$

Where r_d = estimate of annual productivity based on discrete growth, r = the instantaneous rate of increase and t = time in years.

Distribution

Brant wintering in Boundary Bay have recently extended their winter range to include Roberts Bank. In terms of management, it may be important to determine the extent that Brant are using Roberts Bank, if the use is increasing, and if Roberts Bank is used by a specific component of the population. Using Z-tests (Zar 1974), the mean daily numbers and population composition data from each site were compared to see if the wintering population was randomly distributed. Leg-band data were used to determine if breeding ground origin influenced distribution. The proportion of Brant from each breeding ground was transformed using the arcsine$\sqrt{p}$ transformation (Zar 1974) and tested with ANOVAs.

Harvest

The impact of the spring hunt (March 1-10) is an important management issue for Brant wintering in Boundary Bay and Roberts Bank and to other wintering populations on the Pacific Flyway. To estimate the number of Brant shot from each wintering area I constructed a

population profile of Brant present in Boundary Bay and Roberts Bank. To do this leg-band data were collected during three 10-day observation periods, before, during and after the hunting season. For each period I identified the wintering ground affiliation of observed individual bands using leg-band sighting data collected throughout the Pacific Flyway (Washington, Oregon, California, and Mexico). Therefore, for each 10-day period, I was able estimate the proportion of Brant that had wintered in Boundary Bay and Roberts Bank compared to the proportion of spring migrants from Washington, Oregon, California and Mexico. Using the population profile I was able to identify when spring migrants arrived in Boundary Bay and Roberts Bank. To determine if the timing of arrival of migrants was different each year I conducted a chi-square frequency analysis on the leg-band data (Zar 1974).

Using the population profile I was also able to estimate how many birds from each wintering area were harvested during the British Columbia Brant hunting season. I pooled the data from the 10-day periods before and during the hunt across the three years of study. By pooling the data I estimated the maximum numbers of Brant from each wintering area that were susceptible to hunting. I expressed these numbers as proportions of the average number of Brant harvested during the hunt and as proportions of each of the respective wintering populations. I assumed that 8-10% of Black Brant in the Pacific Flyway Brant Population was banded and bands were equally represented in each wintering area. This assumption was based on leg-band observations collected from wintering areas in British Columbia, Oregon, and California. The proportion of banded Black Brant at each wintering area was consistent as was the mix of birds from each of the Arctic breeding and moulting areas (Lee unpubl. data, Morrow unpubl. data, Pitkin unpubl. data, Reed 1997). This mixing is consistent throughout the Flyway; therefore, it is reasonable to assume the band distribution is also consistent. Grey-bellied Brant were not banded at the time of this study and therefore excluded from the analysis (see Appendix A for assumptions and calculations).

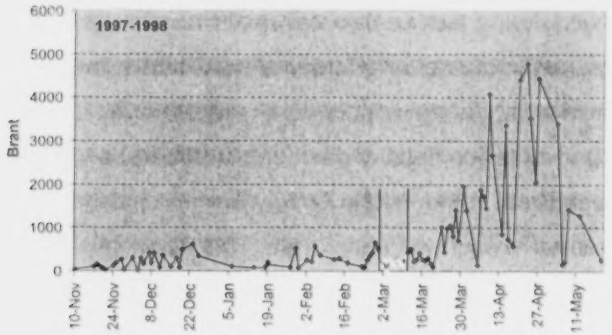
2.3 Results

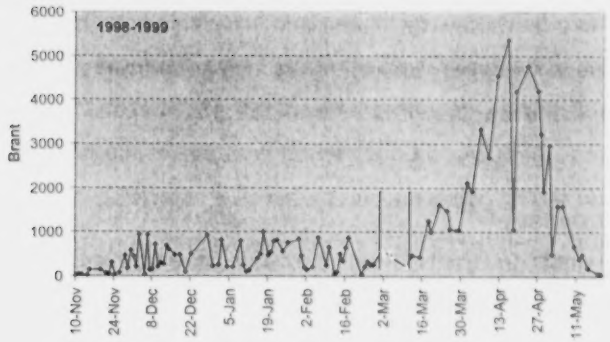
2.3.1 Abundance

The maximum number of wintering Brant observed in Boundary Bay and Roberts Bank for each winter period was 619 (Dec 23, 1997), 985 (Jan 17, 1999) and 1238 (Dec 17, 1999) (Figure 3). The estimates of cumulative Brant goose-days showed that Boundary Bay and Roberts Bank supported increasing Brant usage each year (Table 1).

Table 1. Indices of Brant abundance and cumulative Brant goose-days for each year (15 December to 31 January).

Index	Year					
	1997-98	95% CI	1998-99	95% CI	1999-2000	95% CI
Number of Surveys	16	*	26	*	26	*
Cumulative Goose-days	18416	*	37529	*	54094	*
Mean Count	225.9	93.6	506.0	103.1	690.4	110.2
Maximum Count	619	*	985	*	1238	*





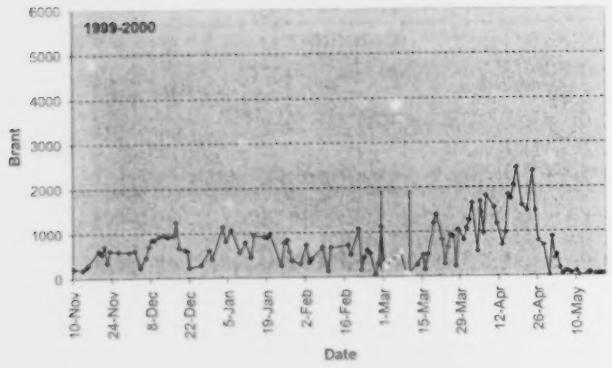


Figure 3. Maximum daily number of Brant in Boundary Bay and Roberts Bank. White points between the two bars indicate surveys conducted during the Brant hunt (March 1-10).

2.3.2 Population Composition and Increase

Population composition is shown in Table 2. The results from Equations 2a-c are in Table 3 and demonstrate that Equation 2c best predicts population increase.

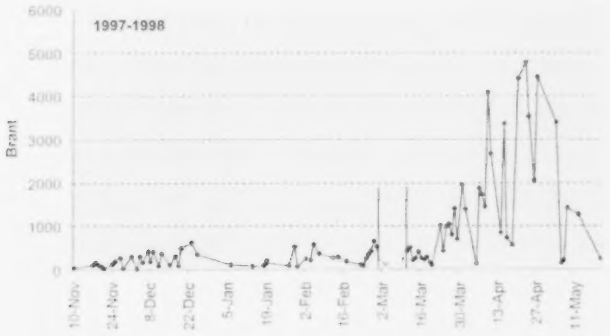
Table 2. Population composition of Brant wintering in Boundary Bay (BB) and Roberts Bank (RB).

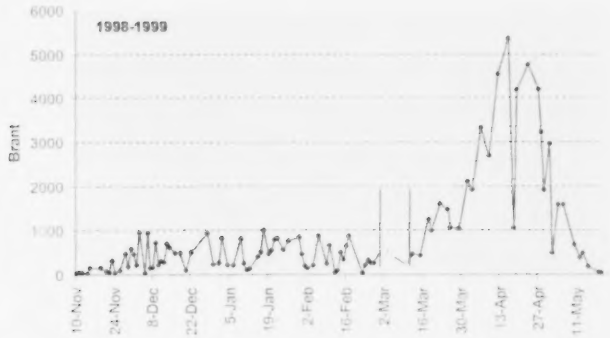
		BLACK		IMMATURE BLACK		GREY-BELLY		IMMATURE GREY-BELLY	
Year	Site	%	95% CI	%	95% CI	%	95% CI	%	95% CI
1997-98	BB	86.6	3.6	7.3	1.4	13.4	7.2	*	*
	RB	*	*	*	*	*	*	*	*
	BB&RB	*	*	*	*	*	*	*	*
1998-99	BB	85.4	3.2	9.7	2.2	14.6	6.4	*	*
	RB	97.0	1.1	45.1	9.4	3.0	2.2	*	*
	BB&RB	88.7	2.2	17.2	5.2	11.3	4.6	*	*
1999-2000	BB	80.5	3.0	16.1	1.2	19.5	3.0	27.6	13.8
	RB	93.3	5.4	34.7	7.2	6.7	5.4	60.0[1]	*
	BB&RB	81.9	3.0	19.6	3.8	18.1	3.0	27.9	12.6

*indicates no data, [1] this estimate based on one sample only, others based on minimum n = 20.

Table 1. Indices of Brant abundance and cumulative Brant goose-days for each year (15 December to 31 January).

Index	Year					
	1997-98	95% CI	1998-99	95% CI	1999-2000	95% CI
Number of Surveys	16	*	26	*	26	*
Cumulative Goose-days	18416	*	37529	*	54094	*
Mean Count	225.9	93.6	506.0	103.1	690.4	110.2
Maximum Count	619	*	985	*	1238	*





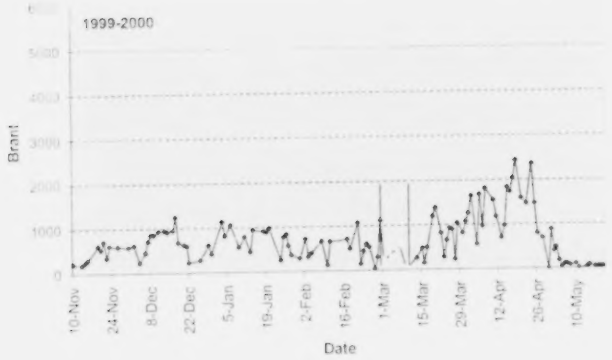


Figure 3. Maximum daily number of Brant in Boundary Bay and Roberts Bank. White points between the two bars indicate surveys conducted during the Brant hunt (March 1-10).

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Year	Site	BLACK		IMMATURE BLACK		GREY-BELLY		IMMATURE GREY-BELLY	
		%	95% CI	%	95% CI	%	95% CI	%	95% CI
1997-98	BB	86.6	3.6	7.3	1.4	13.4	7.2	*	*
	RB	*	*	*	*	*	*	*	*
	BB&RB	*	*	*	*	*	*	*	*
1998-99	BB	85.4	3.2	9.7	2.2	14.6	6.4	*	*
	RB	97.0	1.1	45.1	9.4	3.0	2.2	*	*
	BB&RB	88.7	2.2	17.2	5.2	11.3	4.6	*	*
1999-2000	BB	80.5	3.0	16.1	1.2	19.5	3.0	27.6	13.8
	RB	93.3	5.4	34.7	7.2	6.7	5.4	60.0[1]	*
	BB&RB	81.9	3.0	19.6	3.8	18.1	3.0	27.9	12.6

*indicates no data, [1] this estimate based on one sample only, others based on minimum n = 20.

Table 3. Results from Equations 2a-c using maximum and mean indices of abundance. The observed maximums and means are provided for comparison.

	Equation											
	2a				2b				2c			
y =	1997-98		1998-99		1997-98		1998-99		1997-98		1998-99	
	$N_{(y+1)}$	95% CI	$N_{(y+1)}$	95% CI	$N_{(y+1)}$	95% CI	$N_{(y+1)}$	95% CI	$N_{(y+1)}$	95% CI	$N_{(y+1)}$	95% CI
Max	532	*	1017	*	543	*	915	*	615	*	1128	*
Obs. Max	985	*	1254	*	985	*	1254	*	985	*	1254	*
Mean	176	139	488	166	147	149	478	166	234	152	613	188
Obs. Mean	506	103	690	110	506	103	690	110	506	103	690	110

Using maximum counts as the index of abundance, the exponential growth model equation (Equation 4a) was:

$$N_t = 284e^{0.1964t} \qquad \text{(Equation 4a)}$$

where N = population size, 284 = population size at t = 0, t = time in years, and 0.1964 = the instantaneous rate of increase (Figure 4). Using Equation 3 to adjust the instantaneous rate of increase to one based on discrete growth, the estimate of annual productivity was 21.7%.

The exponential growth model equation generated with mean counts (Equation 4b) was

$$N_t = 114e^{0.2274t} \qquad \text{(Equation 4b)}$$

where N = mean population size, 114 = mean population size at t = 0, t = time in years, and 0.2274 = the instantaneous rate of increase (Figure 5). Therefore, the estimate of annual productivity was 25.5%.

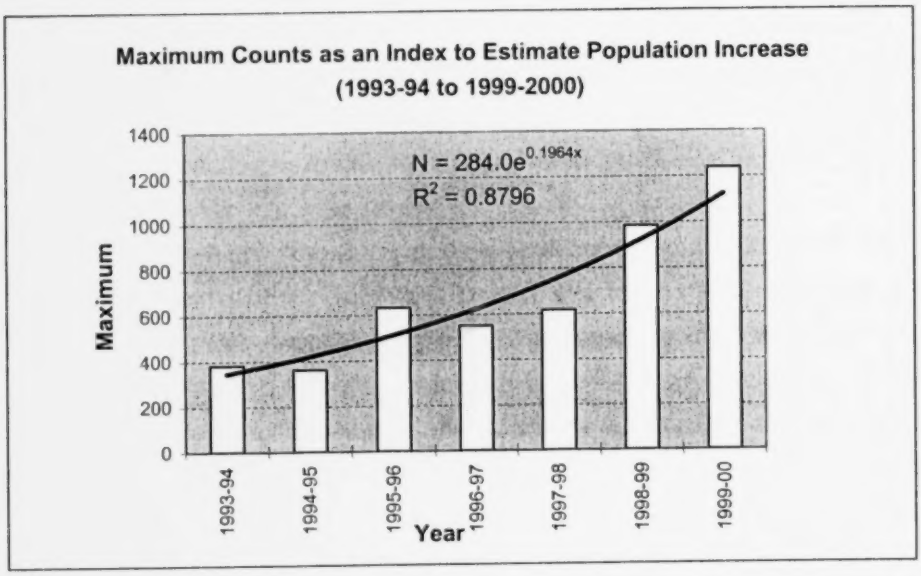


Figure 4. Exponential growth curve model from maximum counts of the Boundary Bay-Roberts Bank Brant population between 1993-94 and 1999-2000 (other data sources: 1993-94 Reed unpubl. data, 1994-95 and 1995-96 Reed 1997, 1996-97 Gowans unpubl. data).

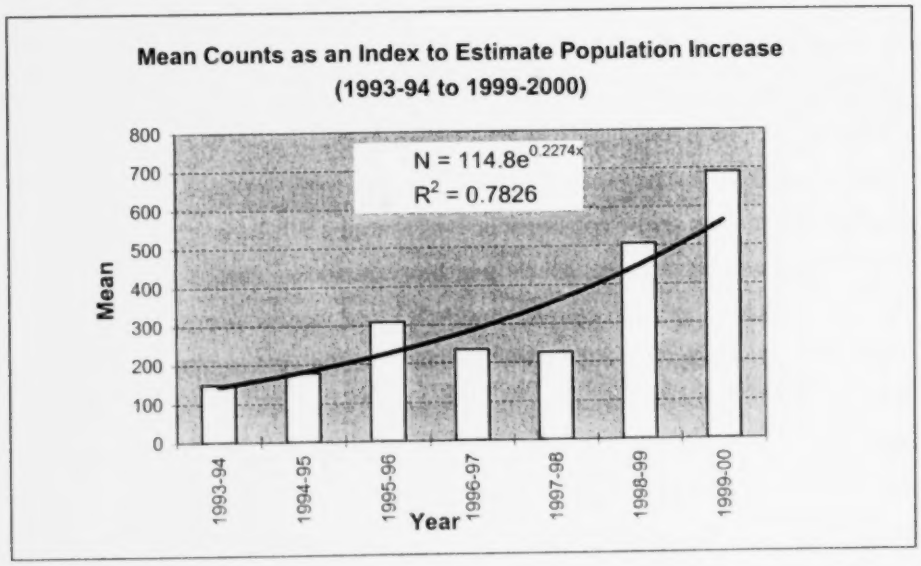
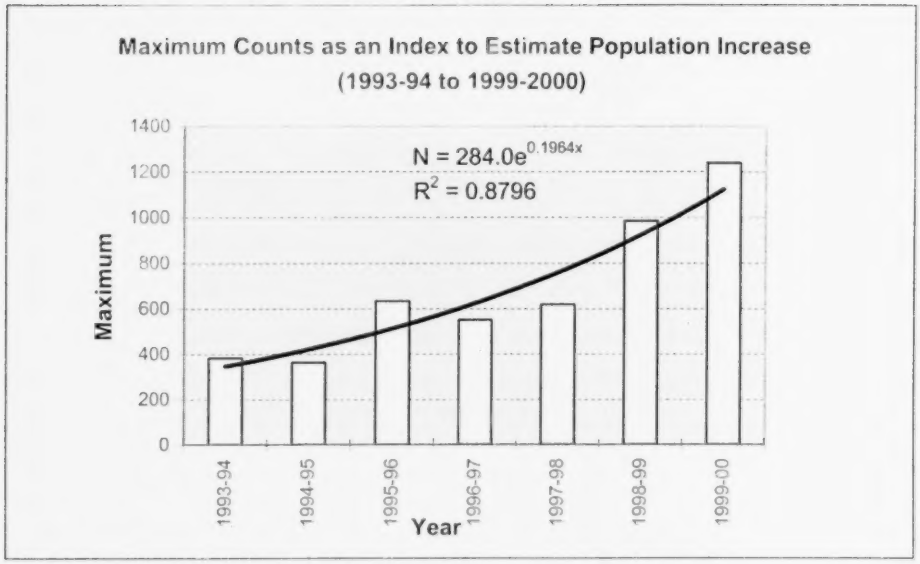


Figure 5. Exponential growth curve model from mean counts of the Boundary Bay-Roberts Bank Brant population between 1993-94 and 1999-2000 (other data sources: 1993-94 Reed unpubl. data, 1994-95 and 1995-96 Reed 1997, 1996-97 Gowans unpubl. report).



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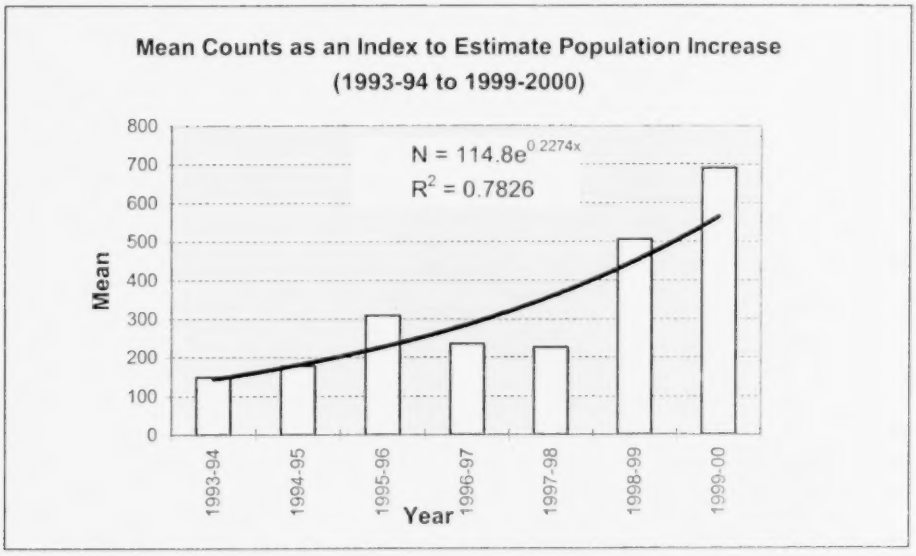

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2.3.3 Distribution

In 1997-98, during regular surveys, Brant were observed at Roberts Bank on only three occasions. In 1998-99 there was no difference in the mean daily use between the two sites (t_{38} = 2.02, p = 0.207), and in 1999-2000, Brant used Roberts Bank more than Boundary Bay (t_{118} = 3.20, p = 0.0017).

In 1998-99 and 1999-2000, larger proportions of immature Brant used Roberts Bank compared to Boundary Bay (1998-99: Z = 6.021, p < 0.0001; 1999-2000: Z = 5.032, p<0.0001). Conversely, larger proportions of Grey-bellied Brant used Boundary Bay compared to Roberts Bank (1998-99: Z = 3.480, p = 0.0003; 1999-2000: Z = 4.146, p < 0.0001). Analysis of the leg band data suggests that site selection was not based on breeding ground origin ($F_{4,24}$ = 0.6831, p = 0.6119) (Figure 6).

2.3.4 Harvest

Counts indicated no increase in the number of Brant in Boundary Bay and Roberts Bank prior to the hunt, suggesting that spring migrants did not arrive before the hunt each year (Figure 3), but leg-band observations suggested otherwise. Birds carrying leg-bands, showing that they had wintered south of BC, were identified in Boundary Bay and Roberts Bank before and during the Brant hunt (Table 4). Over the three years, migrants comprised 21.9% of the population before, 33.1% during and 52.9% after the hunt, strong evidence that migrants were present in the area during the March hunt (Table 4). However, migration appears to have been delayed in the last two years, given that wintering Brant comprised the majority of the birds before and during the hunt (χ^2_2 = 20.56, p < 0.0001). The proportion of migrants was higher in all three time periods in 1998 suggesting that migrants arrived earlier this year than the other years. The largest numbers of migrants were from Mexico, which is to be expected as 90% of Black Brant winter there (Sedinger *et al.* 1994).

During the study, approximately 150-200 Brant were killed during the hunt each year (including crippling mortality) (BC Ministry of Environment Land and Parks unpubl. data and Canadian Wildlife Service unpubl. data). Of these, approximately 70% were estimated to have wintered in Boundary Bay and Roberts Bank (Table 5), hence 105-140 of these Brant were harvested in each hunting season. This is equivalent to 11-15% of the Boundary Bay and Roberts Bank wintering population. Less than 1% of each of the Mexico, California, Oregon and Washington wintering populations were harvested (Appendix A).

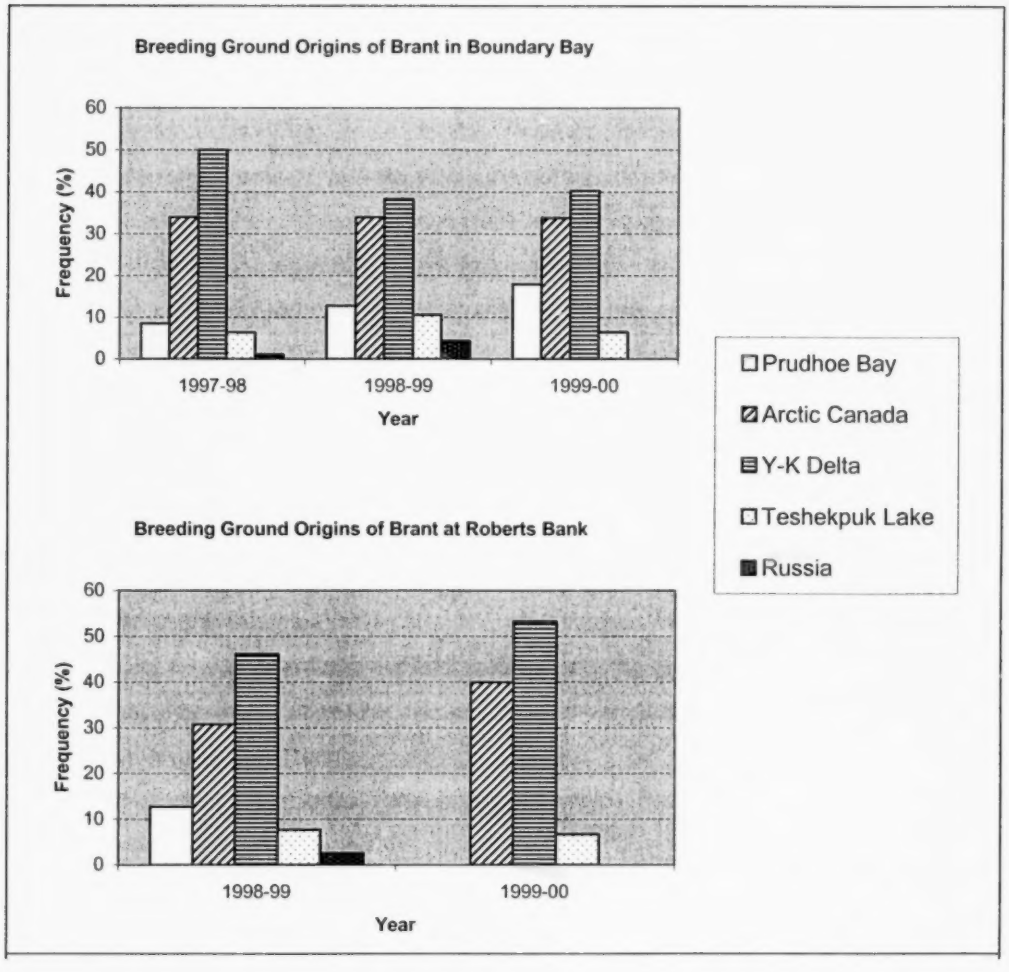


Figure 6. Breeding ground origins of Black Brant estimated from leg-band observations.

Table 4. The number of bands and the composition of Brant observed in Boundary Bay and Roberts Bank classified by wintering affiliation during the 10-day periods before, during and after the hunt.

10 Day Period	Wintering Ground	1998		1999		2000		3-Year Mean
		#	%	#	%	#	%	%
Before	Mexico	11	36.7	1	12.5	1	3.1	17.4
	California	4	13.3	0	0.0	0	0.0	4.4
	Oregon	0	0.0	0	0.0	0	0.0	0.0
	Washington	0	0.0	0	0.0	0	0.0	0.0
	BC	15	50.0	7	87.5	31	96.9	78.1
	Total	**30**	**100.0**	**8**	**100.0**	**32**	**100.0**	**100.0**
During	Mexico	11	42.3	3	23.1	2	10.5	25.3
	California	2	7.7	0.0	0.0	0	0.0	2.6
	Oregon	0	0.0	0.0	0.0	0	0.0	0.0
	Washington	0	0.0	0.0	0.0	3	15.8	5.3
	BC	13	50.0	10	76.9	14	73.7	66.9
	Total	**26**	**100.0**	**13**	**100.0**	**19**	**100.0**	**100.0**
After	Mexico	25	58.1	2	33.3	20	48.8	46.8
	California	3	7.0	0	0.0	3	7.3	4.8
	Oregon	0	0.0	0	0.0	0	0.0	0.0
	Washington	0	0.0	0	0.0	1	2.4	0.8
	BC	15	34.9	4	66.7	17	41.5	47.7
	Total	**43**	**100.0**	**6**	**100.0**	**41**	**100.0**	**100.0**

Table 5. Estimates of the population composition susceptible to hunting in British Columbia and estimates of the number of Brant harvested from each wintering area.

	# Leg-bands Observed From Each Wintering Area 10 Days Before and 10 Days of the Hunt					
	MEX	CAL	OR	WA	BC	T
1998	22	6	0	0	28	56
1999	4	0	0	0	17	21
2000	3	0	0	3	45	51
Total (# of bands)	29	6	0	3	90	128
	22.7	4.7	0.0	2.3	70.3	100
Population Susceptible to Hunting (%)						
Estimated # Brant shot	34-45	7-9	0	3-5	105-140	150-200

MEX = Mexico, CAL = California, OR = Oregon, WA = Washington, BC = British Columbia, T = Total.

2.4 Discussion

2.4.1 Abundance, Population Composition and Increase

During the course of this study, the number of Brant wintering in Boundary Bay and Roberts Bank increased. I suspect two main factors contributed to the increase: 1) annual productivity, and 2) immigration of Grey-bellied Brant. Another factor may be my own improved ability to survey Brant. However, to reduce measurement error and standardize counts, I worked closely with experienced Brant observers and believe the numbers in this study are valid indicators of population change.

I used exponentials models to estimate the annual rate of population increase between 1993-94 and 1999-2000. The estimated rates were clearly higher than the annual productivity as deduced from juvenile ratios (~22% and ~26% compared to mean = 14%, n = 6) (other data sources: Reed 1997, Reed unpubl. data, Gowans unpubl. report).

It was appropriate to use exponential modeling to measure population change because when populations occupy new habitat or rebound from near extinction they are not subjected to limiting conditions and may increase exponentially (Johnson 1994). Exponential increases have been observed in other wintering bird populations recovering from serious declines. Several arctic goose populations have experienced exponential growth after severe population reductions. The Pink-footed Goose *(Anser brachyrhynchus)* of Iceland and Greenland increased from approximately 20,000 geese in the 1950's to over 200,000 in the 1990's (Fox *et al.* 1989). A decline in mortality and improved annual productivity (~18%, n = 25), possibly due to the protection of wintering areas, accounted for the increase (Fox *et al.* 1989). The Svalbard Brant, one of the European stocks of *B.b. hrota* decreased from 40,000-50,000 Brant in the 1890's (Salomonsen 1958) to 1600-2000 in the 1960-70's (Fog 1972). The cause of the decline was likely a combination of over-hunting, uncontrolled egg-collection, and widespread loss of eelgrass due to eelgrass wasting disease (Madsen *et al.* 1999). By the 1990's the population was approximately 6000 birds (Clausen *et al.* 1998) and annual productivity (~15%, n = 16) (Madsen *et al.* 1989) accounted for the increase.

When I examined population composition to determine if annual productivity and/or immigration were responsible for the rapid growth in Brant in Boundary Bay and Roberts Bank, annual productivity did not account for the increases, even in relatively successful years. Equation 2c, incorporating both annual productivity and immigration of Grey-bellied Brant, best predicted population increase. However, Equations 2a-c are too simplified to detect other processes that may be affecting the population. For example, there may be immigration of Black Brant from

other wintering areas. Grey-bellied Brant are showing changes in their wintering distribution and it is probable that Black Brant are making similar shifts.

Although Arctic-nesting geese show high site-fidelity to winter and spring staging sites (Raveling 1979, Prevett and MacInnes 1980, Hestbeck *et al.*1991, Percival 1991), Brant have shown the capacity to make dramatic shifts in their wintering sites (Sedinger *et al.* 1994). Prior to the 1950's, the coast north of Baja, California supported 50-65% of the Pacific Flyway Brant population. Since then, this proportion has decreased to less than 10% of the population, coinciding with an increase in Brant numbers in Baja and along the West Coast of Mexico (Sedinger *et al.* 1994).

Exponential growth cannot occur indefinitely and as a population approaches the carrying capacity of its habitat, the rate of increase will decline (Begon *et al.* 1990). It is not likely that this population is currently subjected to limiting conditions as historically the Fraser River delta supported thousands of wintering Brant and, in addition, the biomass of eelgrass has increased in recent years (Ward *et al.* 1992, Tarbotton and Harrison 1996). However, as the wintering population increases, factors such as intraspecific competition and predation pressure are likely to also increase, leading to changes in the population growth rate. The growth observed in this study is likely the first portion of a logistic curve. Continued monitoring of the wintering population will eventually reveal the maximum number of Brant that can be sustained by Boundary Bay and Roberts Bank. Understanding this growth curve is fundamental for Brant management.

2.4.2 Distribution

During this study Brant in Boundary Bay and Roberts Bank appeared to change their local winter distribution patterns. Daily use of Roberts Bank did not occur until 1998-99, but by 1999-2000 the mean daily number of Brant was higher at Roberts Bank than Boundary Bay. Roberts Bank is subjected to fewer disturbances than Boundary Bay (Chapter 3) and combined with the expansion of eelgrass (Tarbotton and Harrison 1996) may provide Brant with new foraging opportunities. Significantly higher proportions of young were observed at Roberts Bank than at Boundary Bay, whereas, there were higher proportions of Grey-bellied Brant observed at Boundary Bay than at Roberts Bank. Leg-band data showed mixing of Black Brant from the different breeding areas at each site; however, anecdotal behaviour observations suggest the Black and Grey-bellied Brant remained separate and agonistic encounters were common when the two groups were in close proximity.

2.4.3 Harvest

Band observation data suggest that Brant from more southern wintering areas begin to arrive in Boundary Bay and Roberts Bank before the hunting season each year; however, in the last two years of this study, migration appears to have been delayed and wintering Brant comprised the majority of the population during the hunt. This suggests that a) early migrants were not detected in regular counts and, therefore, counts are not a good indicator of when migrants arrive (e.g. Figure 3) and b) timing of migration in relation to the hunt is important to the conservation of wintering Brant.

There are several possibilities as to why Brant numbers do not appear to increase with the initial arrival of spring migrants to Boundary Bay and Roberts Bank. It is likely that some wintering Brant are leaving at the same time as spring migrants are arriving. Mark-resight analysis (Reed 1997) has shown that Brant wintering in Boundary Bay begin to emigrate from the area in early March. The rate of emigration remains constant throughout spring migration. The research also suggested that spring migrants from other areas arrive in Boundary Bay by the third week in February. Therefore, counts do not detect changes in the number of wintering and migrant birds. Migrants may also use areas outside of Boundary Bay and Roberts Bank that are not observed in regular surveys. With the addition of migrants into the area, local distribution patterns of wintering Brant may change such that wintering Brant are more difficult to detect. The distribution of wintering Brant and spring migrants may be critical when examining the band data to estimate harvest. It is possible that migrants entering the area do not initially stage in areas that are accessible for band reading. If this is the case, the band observations will be biased high for winter birds.

During this study, an estimated 11-15% of the Boundary Bay-Roberts Bank wintering Brant population was harvested annually. While this estimate is below the overall rate of increase it is close to the estimate of annual productivity (~14% over 6 years). If there were repeated years of low annual productivity and delayed migration, the hunt could heavily impact the wintering population.

The timing of the BC hunt remains controversial as other states along the Pacific Flyway (e.g. Washington, Oregon, and California) are concerned that their respective wintering populations are harvested during the BC spring hunt. Results from this study suggest that less than 1% of the Brant from each wintering area south of BC are harvested in the BC hunt. However, this estimate does not include the Grey-bellied Brant from Washington State. Furthermore, in this analysis smaller populations are likely to be under-estimated as there is less likelihood of

sighting these bands in Boundary Bay and Roberts Bank. I suspect this may be the case with the estimates of Brant that had wintered in Oregon.

2.4.4 Conclusions and Recommendations

The continued increase in the Boundary Bay-Roberts Bank wintering Brant population is not due to annual productivity alone, but immigration from just south of the Canada-USA border. The most apparent contribution is from the Grey-bellied Brant population that traditionally winters in Washington State. The Boundary Bay-Roberts Bank population has expanded its local winter distribution. Should expansion continue, it may lead to a high degree of connectivity between the BC and Washington populations that cannot be ignored when designing management plans for Brant in BC. Moreover, management plans must consider that the wintering population is comprised of Brant from all the Arctic nesting grounds, and during the spring, from the majority of the wintering areas. Continued monitoring of the Boundary Bay-Roberts Bank population is essential for adaptive management and understanding the processes affecting this and other wintering populations along the Pacific Flyway.

3. BRANT WINTERING IN BOUNDARY BAY AND ROBERTS BANK, BRITISH COLUMBIA: ACTIVITY BUDGETS AND EFFECTS OF DISTURBANCE

3.1 Introduction

Black Brant (*Branta bernicla nigricans*) have historically wintered in large numbers along the coast of British Columbia (Campbell *et al.* 1990). However, over the past 100 years the number of wintering Brant has declined drastically, reaching historic lows in the 1980's (Campbell *et al.* 1990). This was particularly true on the Fraser River delta, near Vancouver, where Christmas Bird Count records show years of few or no Brant during the 1960's to 1980's. Since then, the wintering population increased to approximately 1200 Brant by 2000 (unpubl. data).

In Boundary Bay and Roberts Bank Brant forage on eelgrass (*Zostera marina* and *Z. japonica*) and haul out on spits to preen and ingest grit (Campbell *et al.* 1990). Eelgrass is important to Brant as a primary food source (Cottam *et al.* 1944, Einarsen 1965, Charman 1977, Ganter 2000). Geese have high energy costs and vegetation is generally nutrient-poor so wintering geese need to forage for a large portion of the day to satisfy their energy requirements (Riddington *et al.* 1996).

Farms surround Boundary Bay and Roberts Bank, but increasing residential and commercial development is also encroaching. The associated increase in disturbance to wintering Brant is a management concern. Disturbance is a discrete event that alters the ability of an individual to

obtain resources (White and Pickett 1995). Disturbance may reduce food intake through interruption of foraging bouts or by displacement from feeding areas (Madsen 1985, Bélanger and Bédard 1989). Disturbance may cause changes in behaviour, which can affect distribution, survival and reproductive output and increase energy expenditure from additional time in flight (Madsen 1994, Riddington *et al.* 1996). Time and energy spent responding to disturbance reduces the ability of Brant to feed and perform maintenance activities (Percival and Evans 1997). Geese may abandon a wintering site if the amount of energy they expend outweighs the returns gained from available food resources (Bélanger and Bédard 1989, Stock 1993).

Brant did not consistently use Roberts Bank as a wintering area until 1998-99 (pers. obs). Here, eelgrass biomass has increased substantially (Ward *et al.* 1992, Tarbotton and Harrison 1996) and the area is subjected to fewer disturbances than Boundary Bay. One or both of these reasons may be responsible for the current use of Roberts Bank by Brant.

This study examines activity budgets and the effect of disturbance on wintering Brant in Boundary Bay and Roberts Bank. In doing so the following are addressed:

- energy budgets,
- causes and frequency of disturbance, and
- the effect of disturbance on energy budgets.

Results will help managers understand why local shifts in distribution of wintering Brant have occurred and also identify sources of disturbance for management purposes. Further, findings from this study will help determine if wintering Brant in Boundary Bay and Roberts Bank are being subjected to disturbance levels that might lead to eventual abandonment of the area.

3.2 Methods

3.2.1 Study Area

Boundary Bay and Roberts Bank are 25 km south of Vancouver, British Columbia, on the Fraser River delta (Figure 2). Observations of Brant in Boundary Bay were made from Beach Grove where Brant are frequently found. Two prominent features of Roberts Bank are the Tsawwassen Ferry Terminal and the Deltaport-Westshore Terminal Causeway. Brant haul out on the mudflats between the bases of the two causeways and were observed from shore.

3.2.2 Data Collection

In 1998 and 2000, Brant behaviour was monitored during January and the beginning of February in Boundary Bay. Roberts Bank was surveyed only in 2000. Surveys began at sunrise

or with the arrival of Brant and lasted until sunset or until no Brant remained at the site. Surveys were conducted with a 20-60x spotting scope.

Activity Budgets

Scan-sampling (Altmann 1977) was conducted by scanning flocks of Brant and recording the behaviour of individual birds. Behaviours were classified as swimming, preening, feeding, social, resting and alert (Goudie and Hearne 1994, Stock 1993, Riddington *et al.* 1996). To ensure random sampling, I began scans by focusing the spotting scope at one edge of a flock, recording the behaviour of the bird at the left side of the field of vision, and then adjusting the scope to a new position. I scanned back and forth across the flock for 15 minutes. Each scan was separated by 1-15 minute intervals, the timing determined by randomly generated numbers. Brant in flight were not included.

Disturbance

Causes of disturbance were categorized as natural, human-related, or unknown (Goudie and Hearne 1994, Mooij 1992, Stock 1993, Riddington *et al.* 1996). Specific causes of natural and human-related disturbances were also noted. A disturbance event was defined in terms of a) the length time of the disturbance and b) the effect of the disturbance in terms of distance moved. The length of a disturbance event was defined as the time beginning when 50% of the flock responded by becoming alert and then flying until the time when 50% of the flock returned and resumed normal activity. The time between becoming alert and flying was not measurable (less than 1 second). Distances were recorded as <100m, <200m, <300m, <400m, <500, >500m (still in view), or out of view. All disturbances were recorded whether or not they occurred within a 15-minute scan.

3.2.3 Analysis

Activities were converted into proportions for each scan. The proportional data were transformed using the arcsine$\sqrt{p}$ transformation (Zar 1974). MANOVAs were used to test for differences between years at Boundary Bay and differences between sites for the 2000 data. The tests were Bonferroni adjusted. Activity budgets were converted to energy budgets using the following equation (Wooley and Owen 1978, Gauthier *et al.* 1984, Mooij 1992, Riddington *et al.* 1996):

Energy Expended = (Activity Cost) x (Basal Metabolic Rate) x (% Time of the Activity)

(Equation 5)

On the basis of previous calculations (Owen *et al.* 1992, Wooley and Owen 1978, Gauthier *et al.* 1984, Bélanger and Bédard 1990, Mooij 1992 and Riddington *et al.* 1996) activity costs were assumed to be as follows: resting 1.1 x BMR, preening 2.3 x, feeding 1.7 x, alert 2.1 x, swimming 2.2 x, social 6.4 x and disturbance 15 x. The cost of disturbance was assumed to be equivalent to the cost of flight as flight was always observed as the response to disturbance. Basal metabolic rate (BMR) was calculated as

$$BMR = 327.8 \times W^{.723} \qquad \text{(Equation 6)}$$

where BMR is in kJ/day and W is the mass in kilograms (Lasiewski and Dawson 1967, Riddington *et al.* 1996). Therefore, the BMR for a wintering Brant goose of mean weight 1458 g (Reed *et al.* 1998) was estimated as 430.4 kJ/day.

The daily energy expenditure (DEE) is the amount of energy expended by an individual during average daily activity. DEE is linearly related to BMR; therefore, the larger the bird, the greater the energy expended for daily activities. The relationship between BMR and the theoretical DEE (DEE_t) for an Arctic-nesting goose is (Drent *et al.* 1978, Bédard and Gauthier 1989, Mooij 1992):

$$DEE_t = 2.55 \times BMR \qquad \text{(Equation 7)}$$

Using Equation 7, the DEE_t for a wintering Brant in Boundary Bay and Roberts Bank is predicted to be 1097.5 kJ/day. Sites at which observed DEEs (DEE_o) are above this level may be too energetically demanding for Brant. The DEE_o for each site and year was calculated by summing activity costs. The amount of DEE specifically due to human disturbance was also calculated. The frequency of disturbance, the mean duration, and the mean distance moved in response to disturbance was calculated for each site. T-tests were used to identify differences in disturbance between years at Boundary Bay and between sites in 2000.

3.3 Results

3.3.1 Activity Budgets

In 1998, 63 15-minute scans were conducted at Boundary Bay. In 2000, 69 were conducted at Boundary Bay and 45 at Roberts Bank. Swimming was the dominant activity, followed by

feeding and preening. The remaining time was spent responding to disturbance with small amounts of time resting, socializing, and being alert (Table 6).

Table 6. Time-activity budgets (%) for Brant in Boundary Bay and Roberts Bank.

Behaviour	Boundary Bay 1998 n = 63		Boundary Bay 2000 n = 69		Roberts Bank 2000 n = 45	
	%	SE	%	SE	%	SE
Disturbed	6.7	2.2	10.7	2.5	3.8	0.7
Swimming	44.2	2.4	29.8	2.0	44.9	2.4
Preening	16.5	2.6	26.9	0.7	16.9	1.3
Feeding	31.5	2.4	18.9	0.5	24.4	0.5
Social	0.5	0.1	2.1	0.1	0.5	0.3
Resting	0.2	0.1	0.1	0.0	1.7	0.0
Alert	0.4	0.1	11.5	0.1	7.8	0.0

Overall, time-activity budgets differed across years in Boundary Bay ($F_{7,123} = 78.75$, $p < 0.0001$) and between sites in 2000 ($F_{7,106} = 18.36$, $p < 0.0001$) (Table 7), but there were no significant differences in the total amount of disturbance.

Table 7. F- and p-values from MANOVAs testing differences in time-activity budgets from Boundary Bay (1998 and 2000) and Boundary Bay and Roberts Bank (2000). The Bonferroni adjustment is $p = 0.0073$ for $\alpha = 0.05$.

Activity Tested	Boundary Bay 1998 & 2000	Boundary Bay and Roberts Bank 2000
Overall	$F_{7,123} = 78.75$, $p < 0.0001$	$F_{7,106} = 18.36$, $p < 0.0001$
Disturbed	$F_{1,129} = 2.83$, $p = 0.0950$*	$F_{1,112} = 4.38$, $p = 0.0337$*
Swimming	$F_{1,129} = 10.86$, $p = 0.0013$	$F_{1,112} = 16.96$, $p < 0.0001$
Preening	$F_{1,129} = 13.05$, $p = 0.0004$	$F_{1,112} = 12.53$, $p = 0.0006$
Feeding	$F_{1,129} = 19.70$, $p < 0.0001$	$F_{1,112} = 4.12$, $p = 0.0446$*
Social	$F_{1,129} = 79.75$, $p = 0.0001$	$F_{1,112} = 65.42$, $p < 0.0001$
Resting	$F_{1,129} = 1.19$, $p = 0.2778$*	$F_{1,112} = 8.38$, $p = 0.0045$
Alert	$F_{1,129} = 360.51$, $p < 0.0001$	$F_{1,112} = 9.65$, $p = 0.0024$

* not significant

Table 8 shows the observed DEE in the three samples and the proportion associated with disturbance.

Table 8. Energy costs (kJ/day) for daily activities, total DEE_o and the proportion of the DEE_o due to disturbance (DEE_t for a Brant is 1097.5kJ/day).

Activity	Boundary Bay 1998		Boundary Bay 2000		Roberts Bank 2000	
	Cost	SE	Cost	SE	Cost	SE
Disturbed	432.6	142.0	690.8	161.4	245.3	45.2
Swimming	418.5	22.7	282.2	18.9	425.1	22.7
Preening	163.3	25.7	266.3	6.9	167.3	12.9
Feeding	230.4	17.5	138.3	3.7	178.5	3.7
Social	13.8	2.75	57.8	2.8	13.8	8.3
Resting	0.9	0.5	0.5	0.0	8.0	0
Alert	3.6	0.9	103.9	0.9	70.5	0
Total (DEE_o)	1263.2	212.2	1539.8	194.6	1108.6	92.7
Energy expended if Disturbance removed	830.7	70.1	849.0	33.1	863.3	47.5
Energy for Disturbance (%)	34.2%	11.2%	44.9%	10.5%	22.1%	4.1%

In 1998, disturbance comprised only 6.7% of the time-activity budget in Boundary Bay, but accounted for 34% of the total energy budget (Table 8). In 2000, estimated energy expenditure due to disturbance was 45% in Boundary Bay and 22% in Roberts Bank. The DEE_o for Boundary Bay was greater than the DEE_t in both years, but close to the DEE_t in Roberts Bank in 2000. Subtracting energy costs due to disturbance resulted in totals that were similar in all three cases and below the DEE_t of 1097.5kJ/day.

3.3.2 Disturbance

Natural causes were the most important source of disturbance in both years at Boundary Bay. At Roberts Bank, the largest number of causes was unknown (Table 9).

Table 9. Disturbance (%) at Boundary Bay and Roberts Bank from natural, human and unknown causes.

Cause	Boundary Bay 1998 (n = 91)		Boundary Bay 2000 (n = 106)		Roberts Bank 2000 (n = 37)	
	%	SE	%	SE	%	SE
Human	13.2	2.4	8.5	2.3	11.4*	11.0
Natural	76.9	3.0	61.3	5.7	25.7	8.9
Unknown	9.9	3.1	30.2	6.8	62.9	9.9

*All the human disturbances at Roberts Bank were observed on one day.

Bald eagles (*Haliaeetus leucocephalus*) were the dominant source of natural disturbance, causing 93% (1998) and 97% (2000) of natural disturbances in Boundary Bay and all natural disturbances in Roberts Bank. In both years, the mean frequency of all disturbances was 2.17/hour in Boundary Bay. At Roberts Bank the frequency was significantly less at 1.32/hour ($t_{17} = -2.22$, $p = 0.0199$).

There was no difference in the mean duration of disturbance between years at Boundary Bay ($t_{129} = 1.166$, $p = 0.2456$); however responses to disturbance were longer at Boundary Bay than at Roberts Bank in 2000 ($t_{112} = 2.138$, $p = 0.0340$). There was no difference in the mean distance moved by Brant in response to disturbance either between years at Boundary Bay ($t_{199} = 1.130$, $p = 0.2584$) or between sites in 2000 ($t_{142} = 0.5151$, $p = 0.6073$).

Using estimates for cause of disturbance (Table 9), the amount of energy specifically expended responding to human disturbance was partitioned (Table 10). I assumed the ratio of known human and known natural disturbances was similar in the unknown category. Removal of human-caused disturbance suggests that Brant at Boundary Bay would likely still have a DEE_o above 1097.5kJ/day, but that Brant at Roberts Bank could have a DEE_o below that level (Table 10).

Table 10. Energy expended (kJ/day and % of DEE_o) due to human disturbances, DEE_o with human disturbance removed (Kj/day) and the DEE_t (for comparison).

	Boundary Bay 1998		Boundary Bay 2000		Roberts Bank 2000	
	Cost	**SE**	**Cost**	**SE**	**Cost**	**SE**
Cost of Human Disturbance (kJ/day)	62.7	12.1	76.5	20.0	45.6	30.2
Cost of Human Disturbance as a % of DEE_o	4.9	1.6	4.9	2.7	4.1	2.8
DEE_o – Cost of Human Disturbance (Kj/day)	1200.5	224.3	1463.3	214.6	1063.0	122.9
DEE_t (Kj/day)	1097.5	*	1097.5	*	1097.5	*

3.4 Discussion

The calculation of DEE relies on accurate measurements for activity costs. In this study, these costs were obtained from the literature. There is agreement among most studies on the costs of activities; however, accepted costs for flight range between 8 and 15 x BMR (Tucker 1969, Hart and Berger 1972, Drent *et al.* 1978, Gauthier *et al.* 1984, Bélanger and Bédard 1990, Riddington *et al.* 1996). Long flights are less energy demanding than shorter flights as take-off is the most energy demanding part of flying (Utter and Lefevre 1970, Butler *et al.* 1977). Therefore, in this study, flight caused by disturbance was estimated as 15 x BMR which is consistent with other energetics studies of Arctic-nesting geese (Gauthier *et al.* 1984, Bélanger and Bédard 1990, Riddington *et al.* 1996).

Thermoregulatory costs were assumed to be negligible, as Arctic-nesting geese maintain their body temperature by the heat generated in normal daily activities (West and Norton 1975). This is not the case if the ambient temperature falls below a critical temperature, which was estimated between -2°C and 2°C for Brant (West and Norton 1975, Wooley and Owen 1978, Owen and Reinecke 1977). The average temperatures during this study were 5.0°C (1998) and 6.4°C (2000); however, in both years there were instances when the temperature dropped below -2°C. Therefore, the DEE_o estimates in this study are conservative.

Calculating the DEE_o based on activity budgets is a good method for comparing sites; however, only diurnal observations were made in this study and activity budget analysis did not consider differences between nocturnal and diurnal behaviour. Several studies show geese will feed nocturnally which may compensate for interruptions in diurnal feeding. Feeding comprised a lower proportion of the activity budget at both sites and in both years than has been reported in other studies of Arctic-nesting geese. Mooij (1992) estimated that Bean Geese (*Anser fabalis rossicus*) staging in Germany spent 55% of their time feeding. Other studies show feeding for 47-80% of the day (Gauthier *et al.* 1988, Bélanger and Bédard 1990, Black *et al.* 1991, Riddington *et al.* 1996). Boundary Bay and Roberts Bank experience extreme low nocturnal tides in the winter. During these tides, eelgrass beds are exposed and may provide Brant with foraging opportunities. However, Bélanger and Bédard (1990) showed that in greater snow geese (*Chen caerulescens atlantica*) more than two disturbance events per hour caused an energy deficit that could not be compensated by nocturnal feeding. In Boundary Bay, the frequency of disturbance was 2.17/hour.

On the Yukon-Alaska North Slope staging snow geese that experienced a seasonal average frequency of 0.5 disturbances per hour experienced a 20% decrease in energy reserves (Davis and Wiseley 1974). In Britain, wintering Brent geese doubled their flying time due to disturbance, resulting in a loss of 4.9-11.7% of their daily feeding time and an estimated energy expenditure of 31% (White-Robinson 1982). The frequency of disturbance in Boundary Bay translated to an energy loss of approximately 34% in 1998 and 45% in 2000. The frequency of disturbance at Roberts Bank translated to an estimated energy expenditure of 22%.

Choice of wintering site is determined, in part, by trade-offs between energy gain (from food intake) and energy expenditure (through foraging, maintenance, and movement to and within sites) (Riddington *et al.* 1996). Response to disturbance involves flight, the most energetically expensive of daily activities (Tucker 1969, Hart and Berger 1972, Drent *et al.* 1978, Gauthier *et al.* 1984, Bélanger and Bédard 1990, Riddington *et al.* 1996). Therefore, decreased time available for feeding and increased energy expenditure due to disturbance may result in a change of feeding sites. If alternate sites are not available, birds may respond by increasing their feeding time, feeding at night, increasing their intake rate, processing more efficiently, or by losing weight (Riddington *et al.* 1996).

Preening, alert and social behaviour were comparable with other studies, but in this study, birds spent more time swimming. This is because Pacific Brant are strictly a coastline species; they

do not graze in fields, but only in estuaries and consequently, swimming in shallow waters between feeding sessions is common.

Disturbance also affects the amount of swimming. After a disturbance event, although the flock may have resumed normal activity, Brant tended to swim until they were secure enough to resume feeding again. Alert is another behaviour affected by disturbance. The amount of swimming and alert behaviour that is due to disturbance could not be partitioned in this study, suggesting the estimated impacts of disturbance are conservative (also see Stock 1993).

Predator-like birds with slow wing beats (e.g. Great Blue Heron, *Ardea herodias*) and raptors are the major sources of natural disturbance in a number of other geese-disturbance studies (e.g. Bélanger and Bédard 1989, Ward *et al.* 1994, Riddington *et al.* 1996). The largest identified source of disturbance in this study was from natural causes and in almost all cases was due to Bald Eagles. In most other studies of disturbance, human-related causes were greater than natural ones and management recommendations focused on reducing human impacts.

In this study, the energy expended by Brant due to human disturbance was approximately 4-5% of the DEE_o at each site. At Roberts Bank all the human disturbances were observed in one day. Excluding these, the energy expended at site would likely have been below the DEE_t and demonstrates the importance of managing human disturbance. Levels of disturbance to wintering Brant in Boundary Bay and Roberts Bank are comparable to other studies, but this study showed that disturbance may be above tolerable levels for Brant in Boundary Bay. Because the causes of disturbance at both sites were mainly natural, managing disturbance will be challenging.

Brant have shown the capacity to make large distributional shifts in their wintering areas (Sedinger *et al.* 1994). The most dramatic example of this was the shift in wintering Brant from California to Mexico in the 1950's, which has been attributed to disturbance (Sedinger *et al.* 1994). Brant use of Roberts Bank is a recent phenomenon and may be a consequence of relatively high levels of disturbance and energy expenditure at Boundary Bay.

In order to maintain a wintering population in Boundary Bay and Roberts Bank, disturbance must be managed. The wintering Bald Eagle population in BC is increasing at an annual rate of 8% (CWS unpubl. data). It is possible that disturbance from the growing Bald Eagle population will force the Brant population to abandon Boundary Bay and Roberts Bank within the next 10 years (see Appendix B). Recreational use of Boundary Bay and Roberts Bank will also increase

and controlling the current level of human disturbance may be an essential part of the overall management of disturbance.

For management purposes, more information is required on nocturnal feeding and methods of controlling natural disturbance. In the interim, managing human disturbance may reduce the impacts of disturbance enough to ensure Boundary Bay and Roberts Bank are energetically viable for wintering Brant. However, if the Bald Eagle population continues to increase, no amount of control of human disturbance will compensate for the increase in natural disturbance.

4. SPRING STAGING PATTERNS OF BRANT IN THE STRAIT OF GEORGIA, BRITISH COLUMBIA

4.1 Introduction

Arctic nesting geese are characterized by their sudden arrival to the Arctic to breed and their equally sudden departure in late summer to return to wintering areas (Johnson and Herter 1990). Arctic goose reproductive success is linked with migratory strategies, and spring fattening and nutrient accumulation are essential to their fitness (Ankney and MacInnes 1978, Raveling 1979, Ebbinge 1988, Black *et al.* 1991). During nesting at northern latitudes there are few opportunities for feeding (Ankney and MacInnes 1978). Therefore, geese must reach their Arctic nesting grounds when their body conditions are optimal to meet the demands of egg-laying, incubating and rearing broods (Ankney and MacInnes 1978, Raveling 1979, Ebbinge 1988, Black *et al.* 1991).

Geese build up their nutrient reserves on staging areas during migration. The importance of a particular winter or spring staging area is often assessed by the volume of birds using that area. Volume can be defined as the total number of birds using a stopover site (Thompson 1993, Frederiksen *et al.* 2001). For static populations (e.g. wintering birds), volume estimates are readily obtained through counts, but for transient populations (e.g. migrating birds) estimating volume is more complex (Frederiksen *et al.* 2001) and requires incorporation of estimates of arrival and residence times.

Recently, volume estimates of Arctic geese have been produced through statistical (e.g. Routledge *et al.* 1999) and modeling approaches (e.g. Frederiksen *et al.* 2000). The statistical approach is computationally complex and uses the mean length of stay to estimate total volume. Since length of stay varies among individuals (van Eerden *et al.* 1991), a mean value is not a good estimator and may bias volume estimates and underestimate uncertainty in the calculation of volume. The modeling approach uses capture-mark-recapture (CMR) information that

provides probability estimates of immigration and emigration among multiple staging sites for specific time periods (i.e., weekly intervals), which can be used to calculate lengths of stay per site and per time period. Program MARK (White and Burnham 1999) provides a methodology to calculate such probabilities. I used Program MARK's multi-strata modeling option (described in detail below) that synthesises the dynamics of survival probabilities, resighting probabilities and movement among site probabilities for weekly time intervals to analyze my mark-resighting data. The results, together with counts for time periods, yield robust estimates of length of stay, and volume, and the associated uncertainty of these estimates (Frederiksen *et al.* 2001).

CMR models require repeated observations of marked birds in a population. Black Brant have been marked with individually coded, coloured leg bands on their breeding and moulting grounds since 1985 (Bollinger unpubl. data). Consequently, 8-10% of the Pacific Flyway Brant Population has been marked with leg bands, which can, and have been, identified by observers at spring staging locations (Reed 1997).

Arctic-nesting geese exhibit high philopatry (i.e. the tendency of individuals to exhibit long term fidelity to a specific area) (Greenwood 1980). One consequence of philopatry is local adaptation to specific sites. Hence, changes to, or loss of, staging areas can be detrimental to goose populations. In the Strait of Georgia, numbers of spring-staging Black Brant (*Branta bernicla nigricans*) begin to increase in late February and reach a peak by late March or early April. The two main staging areas in the Strait of Georgia are the Fraser River delta on the British Columbia Lower Mainland and the Parksville-Qualicum area on the east coast of Vancouver Island. High philopatry (81% and 87% respectively) has been observed across years in Brant on these staging grounds (Reed 1997).

A contemporary challenge for conservationists is the management of the Strait of Georgia for the sustainability of Brant as the Strait is undergoing increasing development and urbanization. Consequently, one objective of this study was to estimate the total number of Brant using the Fraser River delta and Parksville-Qualicum as staging areas, and estimate what proportion of the Pacific Flyway Brant Population uses these areas. In doing so, I examined the population composition at each site and the differences in migration and staging patterns between each site.

4.2 Methods

4.2.1 Study Area

The study was conducted at two sites, the Fraser River delta and the east coast of Vancouver Island. Specific areas in the Fraser River delta included Boundary Bay and Roberts Bank in British Columbia and Point Roberts in Washington State. On Vancouver Island, the study area was concentrated between Parksville and Qualicum (Figure 2).

To facilitate the multi-strata model structure I needed to define two other study sites. Although no data were collected at these sites, they were required in order to model the northern migration through the Strait of Georgia. The first site was defined as all areas south of the Strait of Georgia, where Brant migration begins. The final site was defined as all areas north of the Strait of Georgia, where Brant migration ends. Hence, four sites, or strata (A to D) were defined for the study:

A = South - where Brant begin their migration,

B = Fraser River delta - staging area during migration,

C = Parksville-Qualicum - staging area during migration, and

D = North - where Brant end their migration.

4.2.2 Data Collection

Daily surveys were conducted from mid-February until mid-May in 1999 and 2000. Each survey consisted of driving a specific route to check locations where Brant could be observed. A 20-60x spotting scope was used to read leg-bands and conduct counts. The total number of Brant was estimated for each survey day. On Vancouver Island, additional surveys were conducted on a weekly basis between Parksville and Campbell River. These surveys encompassed the Parksville-Qualicum study area and all areas north to Campbell River. The Parksville-Campbell River surveys were only done to determine if Brant staged outside of the Parksville-Qualicum area, and were not included in the MARK analysis. Population composition data were collected by scanning groups of Brant (usually ~100 birds) and counting the number of immature Brant, coloured leg-bands and Grey-bellied Brant (see Chapter 2 for detailed methodology).

4.2.3 Counts

Using the daily abundance estimates, Brant goose-days were calculated for the Fraser River delta, Parksville-Qualicum and Parksville to Campbell River using the formula:

$$\text{Goose-days} = \sum_i \frac{N_i (D_{i+1} - D_{i-1})}{2} \qquad \text{(Equation 1)}$$

where N_i = population at i^{th} survey, D_i = date of i^{th} survey, D_{i+1} = next survey date, and D_{i-1} = previous survey date (Boyd 1995). By definition, $D_0 = D_1$ and $D_{n+1} = D_n$ (Boyd 1995).

To estimate population composition on the Fraser River delta and Parksville-Qualicum, the samples of immature, Grey-bellied, and leg-banded Brant were converted to ratios, and the overall estimate was calculated for each group at each site using the Jackknife technique (Cochran 1977).

4.2.4 Model Data Sets

The CMR data from the leg-band observations on the Fraser River delta and Parksville-Qualicum were analyzed using the multi-strata model option provided by Program MARK (White and Burnham 1999). This model infrastructure facilitated the construction of a model of spring migration as Brant moved from the south, onto the staging areas of the Fraser River delta and Parksville-Qualicum, then to the north. The model provided an opportunity to challenge the CMR data with competing hypotheses concerning migration dynamics. For example, I tested if migration rates change weekly, and if birds moved between the Fraser River delta and Parksville-Qualicum.

Given that Program MARK has a limit to the amount of data it can accommodate, some consolidation of the data was necessary so that Program MARK could test the competing migration hypotheses. My choice was to analyze the data for each year in separate analyses. For both 1999 and 2000, leg-band observations were divided into 7-day periods, a compromise between a loss of resolution in the raw data, and a manageable amount of data and associated parameters for analysis. A total of 15 periods covered the weekly periods from mid-February until the end of May. Weekly periods corresponded across years and strata.

Based on initial data exploration (Appendices C and D), within a year, leg-band data were divided into two groups and modeled separately. Group one contained band data for Brant observed only once within a year (hereafter referred to as single-sight data), and group two contained bands for birds observed multiple times (hereafter referred to as multiple-sight data). These groups represented two distinct staging patterns that were consistent with previous observations of Brant staging in the Strait of Georgia (e.g. Routledge *et al.* 1999).

4.2.5 Multi-strata Model Notation

Model notation followed Cooch and White (1998) where the strata (s) are defined by letters A to D as previously defined. Sighting probabilities were defined as:

p_i^s = the probability that a marked bird present in stratum s at time i is sighted at time i.

Transition probabilities between strata were defined as:

Ψ_i^{rs} = the probability that a bird present in stratum *r* at time *i* is in stratum *s* at time *i*+1.

Survival between strata was defined as:

$$\Phi_i^{rs} = S_i^r \Psi_i^{rs}$$

where the probability of individual survival S_i^r was always assumed to be 1 as mortality during the low-risk staging tenures is considered insignificant (Hestbeck *et al.* 1991, Reed 1997), therefore $\Phi_i^{rs} = \Psi_i^{rs}$.

4.2.6 Assumptions

Several standard and specific assumptions were made in order to model the data. The standard assumptions for CMR analysis included (Seber 1982, Pollock *et al.* 1990, Hestbeck *et al.* 1991):

a) every marked animal present in the population at time *i* had the same probability of being observed, p_i,
b) all samples were instantaneous relative to the interval between *i* and *i*+1,
c) individuals and individual fates were independent,
d) marking of individuals was random,
e) there were no behavioural effects from marking,

and further assumptions specific to these analyses included:

f) leg-band data sets contained no observation errors,
g) mortality between weekly time periods was insignificant (i.e. survival = 1),
h) the probability of sighting on Stratum A = 1, because an individual was considered in Stratum A until it was observed in either B or C
i) the probability of sighting on Stratum D = 1, because an individual was considered in Stratum D when it was no longer observed in either B or C,
j) once in Strata B or C individuals could not return to A (i.e. spring migration was consistently north), and
k) once in Stratum D, individuals did not return to B or C (i.e. spring migration was consistently north).

When modeling the migration of Arctic-nesting geese, standard CMR assumptions are often violated (Hestbeck *et al.* 1991, Anderson *et al.* 1994). Geese exhibit strong bonds between mates and families migrate as cohesive units (Prevett and MacInnes 1980, Reed 1993). Fates of pairs and families are closely linked and violate the assumption of independence. Marking of individuals is not random as families are captured and marked together. Therefore, the true

effective sample size is smaller than the actual number of marked birds and results in an underestimation of variance (Schmutz *et al.* 1995).

These violations are reflected in my results by high values of ĉ (variance inflation factor). A ĉ value = 1 indicates independence and non-violation of standard assumptions as tested by GOF tests, i.e., random binomial error. Values larger than 1 suggest overdispersion of the data, i.e. the clumping of individuals such that a ĉ value of 2 implies that birds are acting and making decisions as a pair. This is a reasonable expectation for Arctic-nesting geese and is observed in many species, which migrate as schools or flocks (Anderson *et al.* 1994).

Assumptions *h* and *i* were necessary in order to create the appropriate encounter histories to be read by Program MARK. However, this meant it was possible for a bird to either arrive on Strata B or C from A before it was actually observed, or to still be present on Strata B or C although it was assumed to have departed for D. To adjust for these possibilities, an *a posteriori* correction was applied to the results for the multiple-sight data models so that I could more accurately estimate arrival and departure dates to and from Strata B and C, and also length-of-stay.

4.2.7 Migration Model Construction and Selection

The multi-strata models are an extension of the generalized CMR model (the Cormack-Jolly-Seber model), and allow for the estimation of transition probabilities between strata (Brownie *et al.* 1993, Hestbeck *et al.* 1991). In this study, strata refer to geographic locations along a migration route. A data record for a single bird as it is sighted at specific intervals (e.g. weekly) along its migration route is called an encounter history. A complete encounter history records the stratum where the bird is seen in a particular week, e.g. AAAB0BB0CCCDDDDD, where 0 represents no sighting. Using the Multi-strata Recaptures Only option in Program MARK, I used separate models for each year to estimate transition probabilities for the following movements:

Single-sight (1999, 2000):

- A to B
- A to C

Multiple-sight (1999, 2000):

- A to B
- A to C
- (B,C) to (B,C,D)

I was fortunate that only on four occasions was a bird seen at more than one stratum within a single week. I dealt with that data issue by randomly choosing (coin toss) one of the strata for that period. I challenged the data by statistically fitting hypothesized competing models that described the pattern of the transition probabilities among strata over time. I then chose the best models based on the Quasi Akaike Information Criterion ($QAIC_c$), which takes into account the extra-binomial dispersion of error variance resulting from the non-independent behaviour of individual birds (Anderson *et al.* 1994, Burnham and Anderson 1998)

Program MARK is not capable at this time of performing a parametric bootstrap goodness-of-fit (GOF) test for multi-strata models. Therefore I conducted non-parametric bootstraps of the observed data to simulate deviances (Schwarz *et al.* 1993). I compared the $\hat{c}$ for my data to the distribution of $\hat{c}$ values generated by simulations to judge the probability of my data. That is, I was asking the question "could my data have reasonably been generated by the model I selected based on QAIC?" To compute $\hat{c}$ I took the observed and expected deviance values for the encounter histories in the data and used the equation (White 2000):

$$\hat{c} = 2\sum_{i=1}^{n} O_i \ln(O_i / E_i) \qquad \text{(Equation 8)}$$

where O_i = observed and E_i = expected frequencies of the observed encounter histories, subject to the constraint that and $\Sigma\ O_i = \Sigma\ E_i$ over all possible encounter histories.

4.2.8 Adjusted Arrival and Departure Weeks

Since birds were never observed on strata A or D, I had to assume that birds arrived on strata B or C the first week they were observed, and arrived on stratum D the week after they were last seen on B or C. Therefore p_i^A and p_i^D (i.e., the probability of being on strata A or D, respectively in weekly period 1) were fixed at 1 in all competing models. However, it was possible, and even somewhat likely, that a bird arrived on strata B or C from A before it was observed in B or C. Conversely a bird not seen on B or C and necessarily assumed to have left for D, may just not have been observed on B or C. To correct for these *a priori* assumptions I made *a posteriori* adjustments of the time period of arrival for the multi-sight data using the sighting probabilities (p_i^r) generated from the models. These adjustments were not applied to the single-sight data, since I chose to define birds in the single-sight category as those that were observed to arrive and depart within the one-week time period in which they were observed.

The revised estimate of the week of arrival was estimated using the following equations:

$$\hat{A} = \sum_{w=1}^{F} wP'_{A,w} \qquad \text{(Equation 9)}$$

where $\hat{A}$ = the estimated period (week) of arrival, F = the first period a marked bird was seen, w = period and $P'_{A,w}$ = the probability that the marked bird arrived in period w or later if it had not been seen prior to F. The term $P'_{A,w}$ was calculated using:

$$P'_{A,w} = P_{A,w} \prod_{i=w}^{F} \left(1 - p_i^r\right) \qquad \text{(Equation 10)}$$

where $P_{A,w} = \left(\frac{1}{N - \sum_{i=1}^{w-1} 1} \right)$ i.e. the probability that the marked bird arrived in period w, given

it had not arrived prior to w, and p_i^r = the probability of a marked bird being seen in period w = 2, ….N, given that it was present. The standard error of Â was estimated as:

$$\hat{s}_A = \sqrt{\sum_{w=1}^{F} w^2 P'_{A,w} - \hat{A}^2} \qquad \text{(Equation 11)}$$

The same approach was used to estimate modified departure times:

$$\hat{D} = \sum_{w=L}^{N} wP'_{D,w} \qquad \text{(Equation 12)}$$

where $\hat{D}$ = the estimated period (week) of departure, L = the last period that the marked bird was observed, and $P'_{D,w}$ = the probability that the marked bird departed in period w or earlier if it had not been seen after period L:

$$P'_{D,w} = P_{D,w} \prod_{i=L}^{w} \left(1 - p_i^r\right) \qquad \text{(Equation 13)}$$

where $P_{D,w} = \left(\frac{1}{N - \sum_{i=w+1}^{L} 1} \right)$ i.e., the probability that the marked bird departed in period w,

given it had not departed later than period w. The standard error of $\hat{D}$ was estimated as:

$$\hat{s}_D = \sqrt{\sum_{w=L}^{N} w^2 P'_{D,w} - \hat{D}^2} \qquad \text{(Equation 14)}$$

4.2.9 Length of Stay

The mean length of stay for an individual Brant goose in the multiple-sight category was estimated for each cohort of birds (where a cohort was defined as the group of birds that arrived in a week period) on each stratum using the probabilities of remaining (R) and leaving (L) a stratum where:

$$p(R_i) = 1 - (\Phi_i^{rs} + \Phi_i^{rt}) \qquad \text{(Equation 15)}$$

$$p(L_i) = 1 - p(R_i)(1 - \sum_{j=1}^{i-1} P(L_j)) \quad \text{for } i < \text{the last week} \qquad \text{(Equation 16)}$$

$$p(L_i) = (1 - \sum_{j=1}^{i-1} P(L_j))) \quad \text{for } i = \text{the last week} \qquad \text{(Equation 17)}$$

and length of stay (T) was calculated as:

$$T = \sum_{i=1}^{k} p(L_i) \qquad \text{(Equation 18)}$$

where i = period, j = period and k = number of periods.

4.2.10 Volume Estimates

Volume estimates were calculated for each stratum by independently estimating, then summing, the number of single-sight and multiple-sight Brant that arrived each period. First, for each period I estimated the abundance from the count data and the proportion of birds that were classified as single-sight or multiple-sight from the band observation data. This led directly to an estimate of the volume of single-sight Brant:

$$\hat{V}_{SS} = \sum_{i=1}^{k} (n_i)(pSS_i) \qquad \text{(Equation 19)}$$

where $\hat{V}_{SS}$ = volume of single-sight Brant estimate, n_i = estimate of period abundance, and pSS_i = the proportion of single-sight Brant in the period.

Second, for each period an estimate of the number of multiple-sight Brant was derived from:

$$M_i = (n_i)(pM_i) \qquad \text{(Equation 20)}$$

where M_i = the number of multiple-sight Brant, n_i = estimate of period abundance, and pM_i = the proportion of multiple-sight Brant in the period.

The total volume of multiple-sight Brant was estimated using M_i and $p(R_i)$:

$$\hat{V}_M = M_{1,1} + \sum_{i=2}^{k} \{M_{i,i} - \sum_{j=1}^{i=1} (M_{i-1,j}\, p(R_{i-1,j})\} \qquad \text{(Equation 21)}$$

where i = index of periods, j = index of cohorts and k = number of periods. The estimate of volume of Brant arriving over all periods is:

$$\hat{V}_T = \hat{V}_{SS} + \hat{V}_{MS} \qquad \text{(Equation 22)}$$

Error in the volume estimates arises from two sources, 1) counting error in abundance estimates, and 2) statistical error in Program MARK's estimates of the transition probabilities. There was no explicit measure of error for abundance estimates as they were from single counts; therefore, I simulated different degrees of error in the volume estimates by imposing three different levels of counting error (5%, 10% and 20%). Due to model complexity I was forced to avoid the computational complexity of trying to precisely estimate the total variance of the volume estimates due to the individual transition probability variances and covariances. Therefore, I present three extreme scenarios to characterize the uncertainty of my estimates arising from uncertainty in the transition probability estimates: 1) no uncertainty in the parameter estimates (extreme underestimation, only uncertainty is due to counting errors), 2) parameter estimates are uncorrelated (overestimate of uncertainty), and 3) parameter estimates are 100% positively correlated (intermediate uncertainty). Simulations were computed 1000 times to obtain randomized estimates. In doing so, the range from no uncertainty to extreme uncertainty in volume estimates was estimated.

4.3 Results

4.3.1 Counts

The peak of migration occurred at similar times each year, but in both years the peak occurred about two weeks later on the Fraser River delta than on Vancouver Island (Figures 7 and 8). The peak abundance and the number of Brant goose-days were lower on the Fraser River delta in 2000 than in 1999 (Table 11). Approximately 5-6% of the Brant observed on the Fraser River delta and about 8-9% of the Brant on Vancouver Island wore leg-bands (Table 12). No Grey-bellied Brant were observed on Vancouver Island.

The Parksville-Campbell River surveys encompassed the Parksville-Qualicum area; however, the surveys were only conducted 1/week. In both years the maximum daily number of Brant observed at Parksville-Qualicum was not during a Parksville-Campbell River survey. Consequently, the Parksville-Campbell River peak count was less than the one for Parksville-Qualicum, although the survey covered a larger geographical area. Overall, the surveys did show that the larger survey area supports a greater number of goose-days than just Parksville-Qualicum (Table 11).

Table 11. Brant Goose-days and peak abundance during spring migration on the Fraser River delta and the east coast of Vancouver Island.

Year	Site	Goose-days	Peak Abundance	Date of Peak Abundance
1999	**FRD**	154519	5347	April 16
	PQ	128949	6900	April 1
	PQ-CR	141452	5226	April 8
2000	**FRD**	67532	2428	April 18
	PQ	150145	5415	March 29
	PQ-CR	156243	4381	April 2

FRD = Fraser River delta, PQ = Parksville-Qualicum and PQ-CR = surveys between Parksville and Campbell River.

Table 12. Proportions (%) of leg-banded, immature and Grey-bellied Brant observed on the Fraser River delta (FRD) and Vancouver Island (VI).

		Leg-banded		Immature Black Brant		Grey-bellied		Immature Grey-bellied	
Year	Site	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1999	FRD	5.3	1.0	21.4	3.8	14.4	2.5	*	*
	VI	8.1	1.3	5.7	0.3	0.0	0.0	0.0	0.0
2000	FRD	6.1	0.4	17.9	1.1	17.3	1.1	26.5	5.1
	VI	8.7	0.5	14.6	1.1	0.0	0.0	0.0	0.0

* no data

4.3.2 Band Observations

In 1999, 1094 discrete bands were observed in Parksville-Qualicum and 316 on the Fraser River delta. In 2000, 900 discrete bands were observed in Parksville-Qualicum and 382 on the Fraser River delta. The most common observations were of single-sight bands, which comprised approximately 40% of Parksville-Qualicum and 70% of Fraser River delta observations (Appendix C).

4.3.3 Program MARK Multi-strata Model Selection

A model that constrained the logit of transition probabilities to conform to a quadratic function of time period was the most parsimonious model for each year of the single-sight data. The two years of single-sight data were treated as different groups within the same model; therefore, the model characteristics generated by Program MARK are identical. A model that constrained the logit of transition probabilities to conform to quadratic functions of both time period and cohort provided the most parsimonious models for the multiple-sight data for each year (Table 13). The high $\hat{c}$ values (~3-6) indicate the data are overdispersed and, as anticipated for reasons explained earlier, clearly violate the assumption of independence in the data.

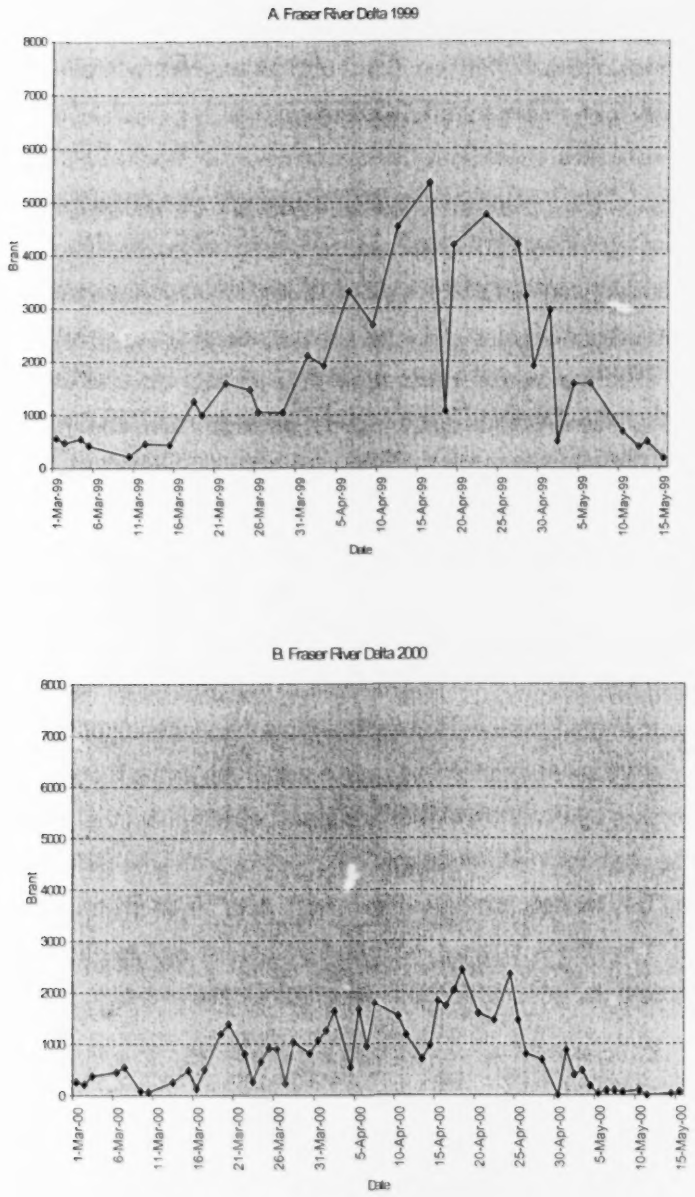


Figure 7. Brant abundance during spring migration on the Fraser River delta. A. 1999. B. 2000.

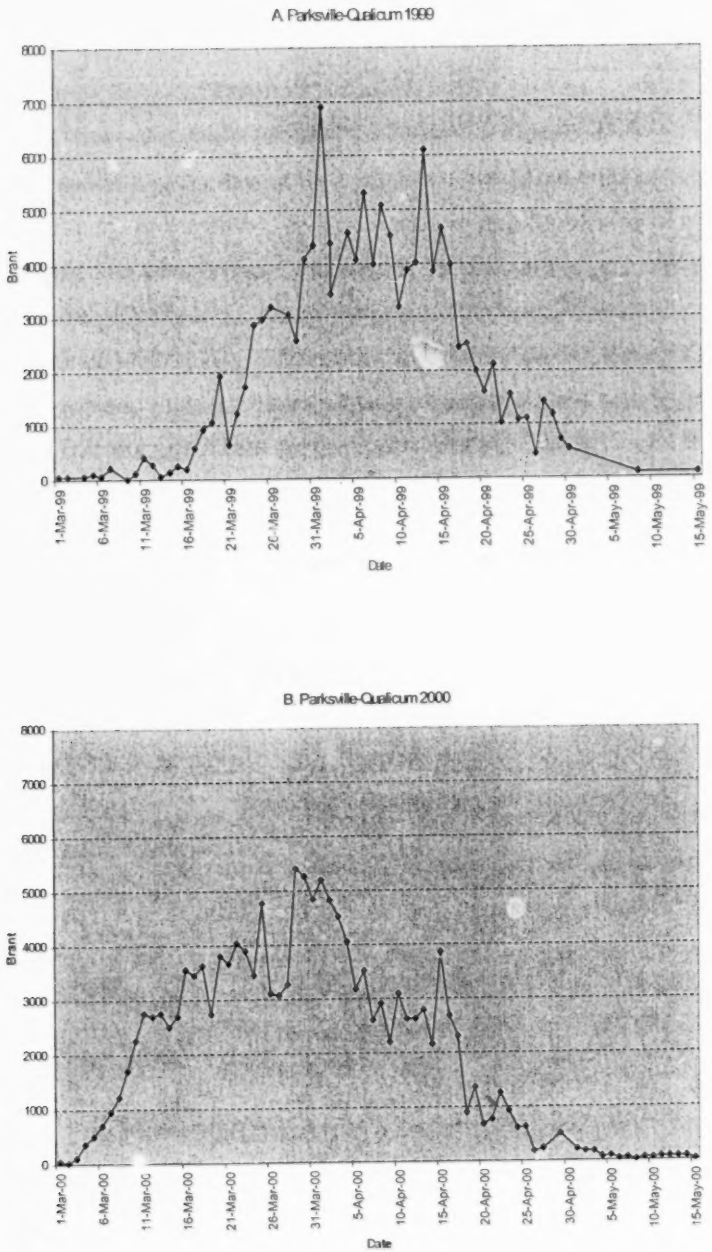


Figure 8. Brant abundance during spring migration in Parksville-Qualicum. A. 1999. B. 2000.

Table 13. Best models for single-sight and multiple-sight data.

Model	Model Characteristics				
	# Parameters	Deviance	QAICc	ĉ	ĉ SE
Single-sight					
1999 from A to B or C	12	221.3	6743.6	6.33	1.97
2000 from A to B or C	12	221.3	6743.6	3.10	0.96
Multiple-sight					
1999 from A to B or C	6	212.3	3421.2	2.67	1.17
2000 from A to B or C	6	992.3	4556.1	4.62	1.61
1999 from B or C to D	27	556.0	2967.1	6.48	0.92
2000 from B or C to D	35	829.8	3580.9	6.20	0.68

Single-Sight Models

Single-sight models were used to estimate transition probabilities from Stratum A to either Stratum B or C for individuals only observed once. These models predicted that early in migration, the probability of moving from Stratum A to Stratum B was low, but as time progressed the transition probability increased (Figure 9). The probability of moving from Stratum A to C was initially low but as time increased, the probability increased until approximately week 8 (Figure 9). These models showed that Brant migrating from Stratum A after week 9 had a higher probability of moving to Stratum B than to Stratum C (see Appendix E for transition probabilities). The second part of the migration movement is from Strata B and C to Stratum D, but by definition, single-sight birds arrive and leave within the same weekly period.

Multiple-Sight Models

Separate multiple-sight models were used to estimate the weekly transition probabilities for each cohort of birds in 1999 and 2000. The first part of the migration was the transition from Stratum A to B or C. In 1999 there was a higher probability of migrating from Stratum A to Stratum C than to Stratum B early in migration. Late in migration, all Brant were expected to

migrate to Stratum B. In 2000, the probability of migrating from Stratum A to Stratum C was higher than to Stratum B with the exception of the last period Brant were observed (week 13) (Figure 10). The highest probability of migrating to Stratum C was similar in both years (approximately week 8). On Stratum B, although the pattern was similar across years, the transition probabilities were much lower in 2000 than in 1999 (Figure 10).

The second part of the migration was the transition from Stratum B or C to D after a length of stay of a week or more at Stratum B or C. In general, the probability of a bird migrating to Stratum D increased as period (time) increased. Hence, a bird that arrived to either Stratum B or C in the first week of migration tended have a longer residence time there than one that arrived later (Figures 11 and 12). Differences existed in the movement patterns through Strata B and C. The models in Figure 11 and 12 show steeper curves with flatter tails for Stratum C compared to B. This suggests that early migrating Brant that arrived in Stratum C, staged longer than those on Stratum B. Limited interchange occurred between Strata B and C. In 1999, 0.5% and in 2000, 3% of the bands were observed at both sites (see Appendix E for transition probabilities).

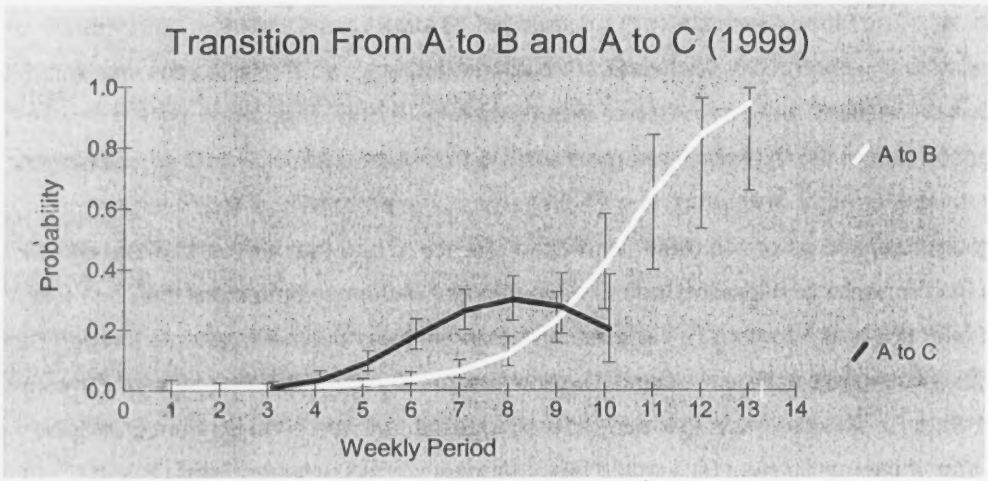
The probably of remaining on Stratum B (or C) in a given week *i*, is the complement to this probability 1- Φ_i^{BD} (or 1- Φ_i^{CD}). The arrival and departure weeks are listed in Appendix F.

4.3.4 Length of Stay

Length of stay for multiple-sight birds generally decreased as the week that a cohort arrived increased (Figure 13) (See Appendix F for associated standard errors).

4.3.5 Volume Estimates

The estimated volumes were similar between years on Stratum C, but decreased between years on Stratum B (Table 14). In 1999 and 2000, the midwinter indices for the Pacific Flyway Brant Population were 119,993 and 127,129 respectively (Pacific Flyway Committee 2001). Table 15 contains volume estimates and their uncertainty from this study expressed as proportions of the Pacific Flyway Brant Population.



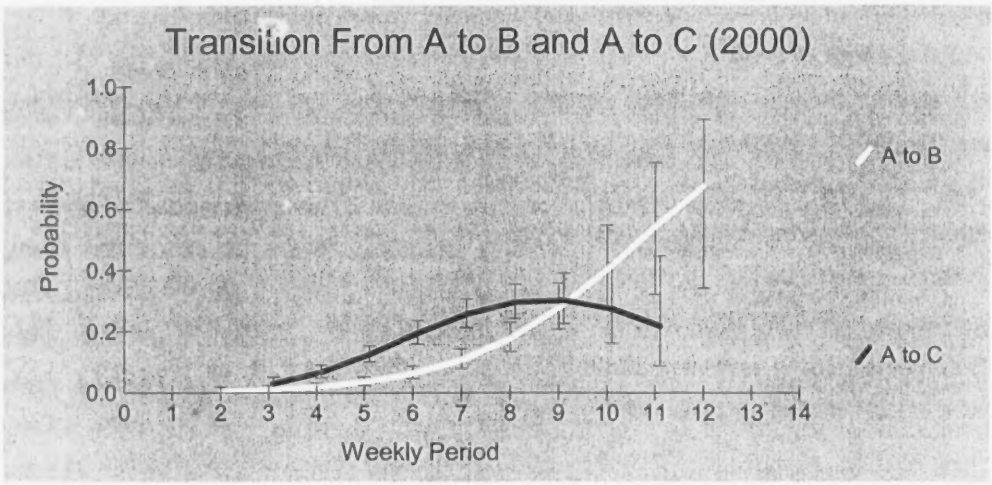
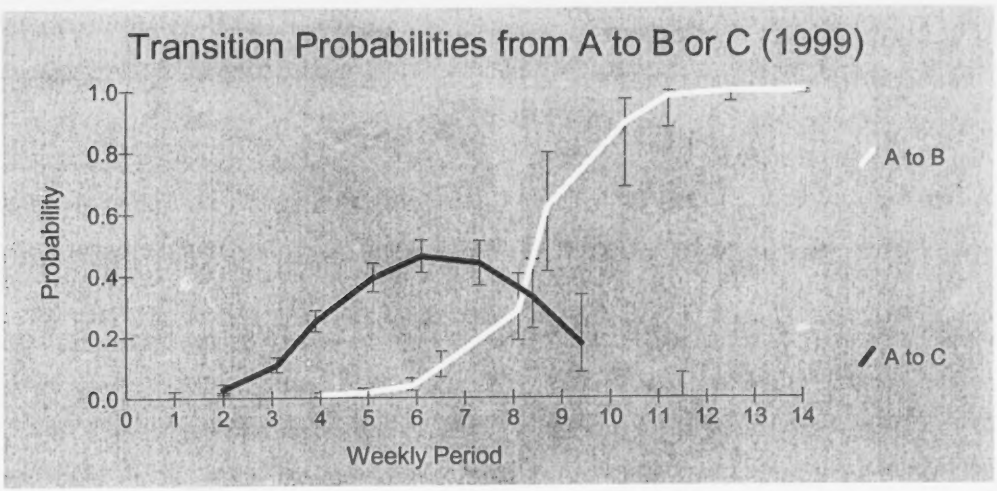


Figure 9. Each curve models the probability of transition from Stratum A to Stratum B or C during each period for single-sight data. The probably of remaining on Stratum A in a given week *i*, is the complement to these probabilities 1- Φ_i^{AB} + Φ_i^{AC}.



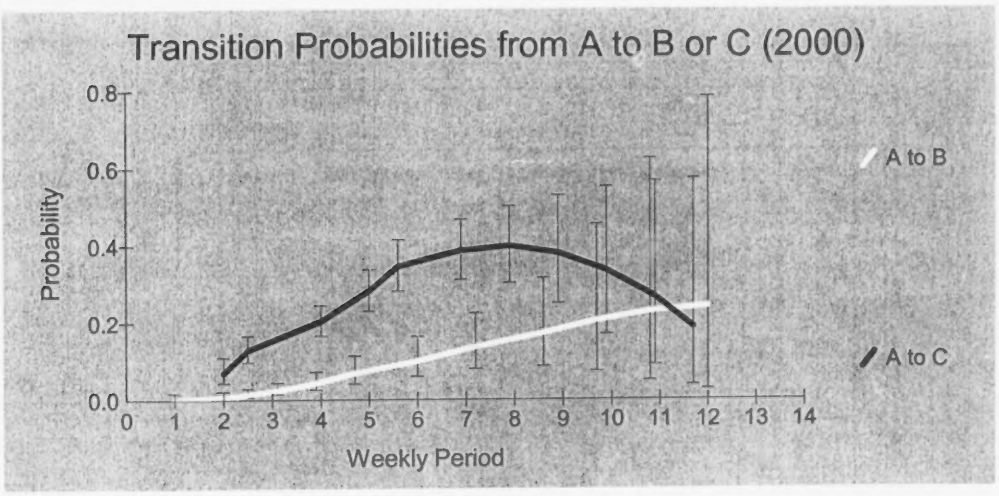
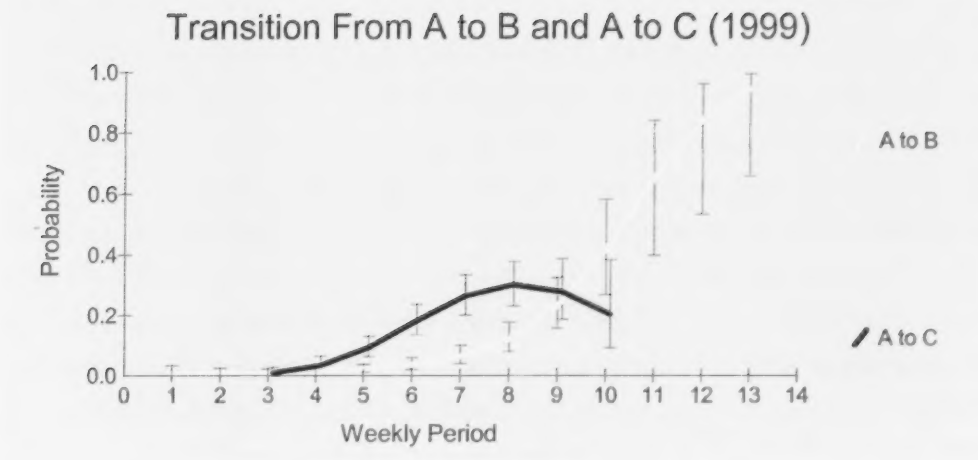


Figure 10. Each curve models the transition probability from Stratum A to either B or C for the multiple-sight data. The probably of remaining on Stratum A in a given week *i*, is the complement to these probabilities 1- $\Phi_i^{AB} + \Phi_i^{AC}$.



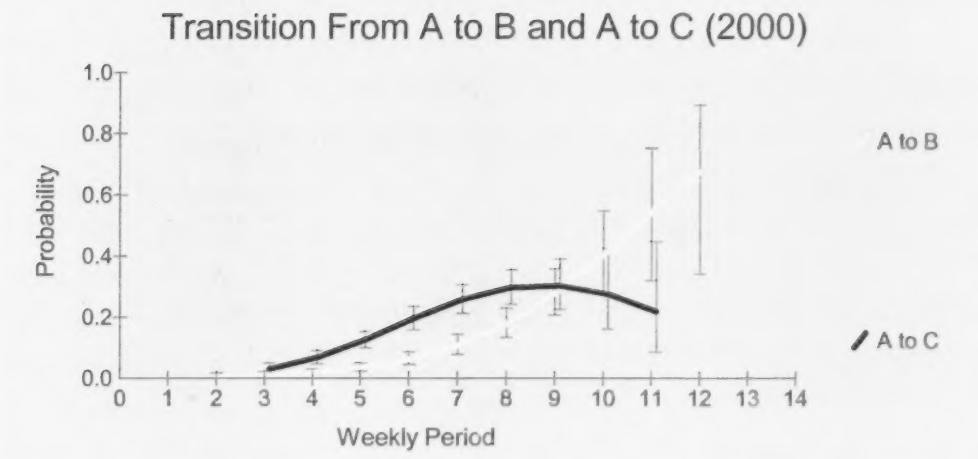


Figure 9. Each curve models the probability of transition from Stratum A to Stratum B or C during each period for single-sight data. The probably of remaining on Stratum A in a given week *i*, is the complement to these probabilities 1- $\Phi_i^{AB} + \Phi_i^{AC}$.

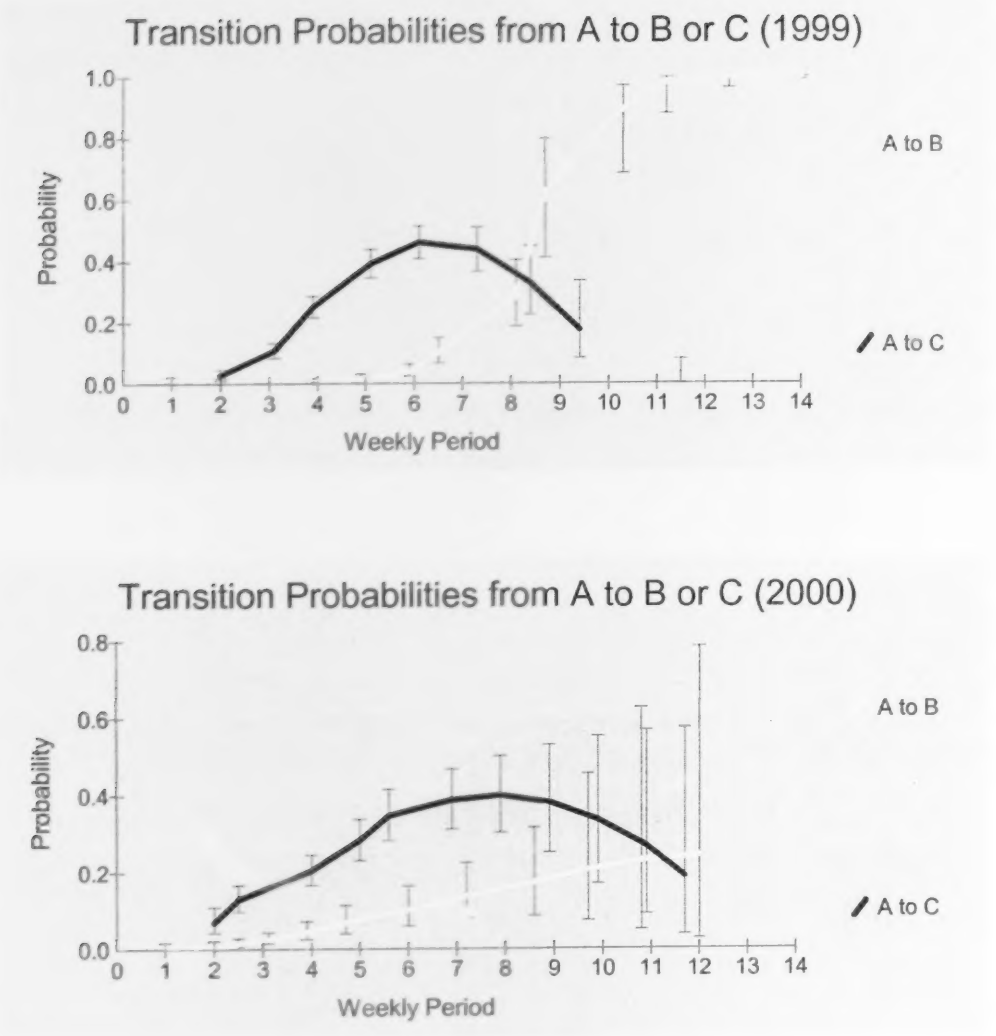
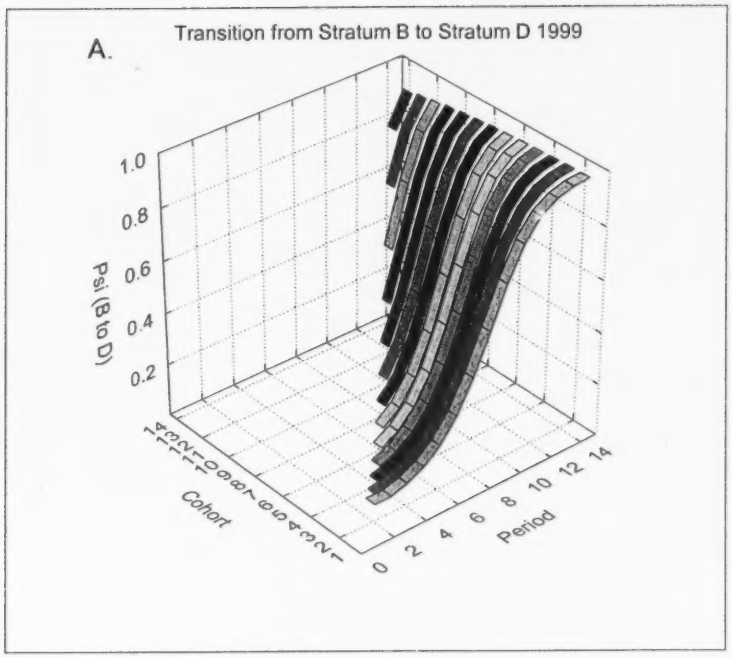


Figure 10. Each curve models the transition probability from Stratum A to either B or C for the multiple-sight data. The probably of remaining on Stratum A in a given week *i*, is the complement to these probabilities 1- $\Phi_i^{AB} + \Phi_i^{AC}$.



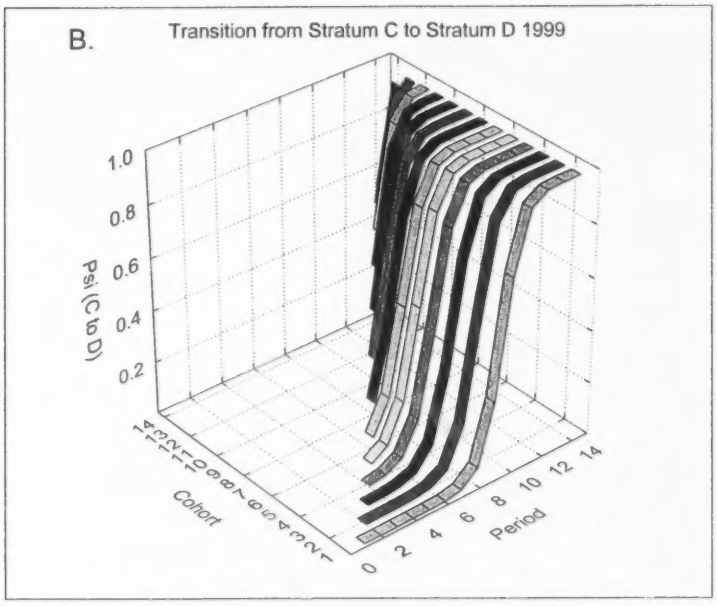


Figure 11. Each graph depicts the transition probability for each cohort of birds, each period, in 1999. A) Transition from Stratum B to D. B) Transition from Stratum C to D. The probably of remaining on Stratum B (or C) in a given week *i* is the complement to this probability 1- Φ_i^{BD} (or 1- Φ_i^{CD}). The arrival and departure weeks are listed in Appendix F.

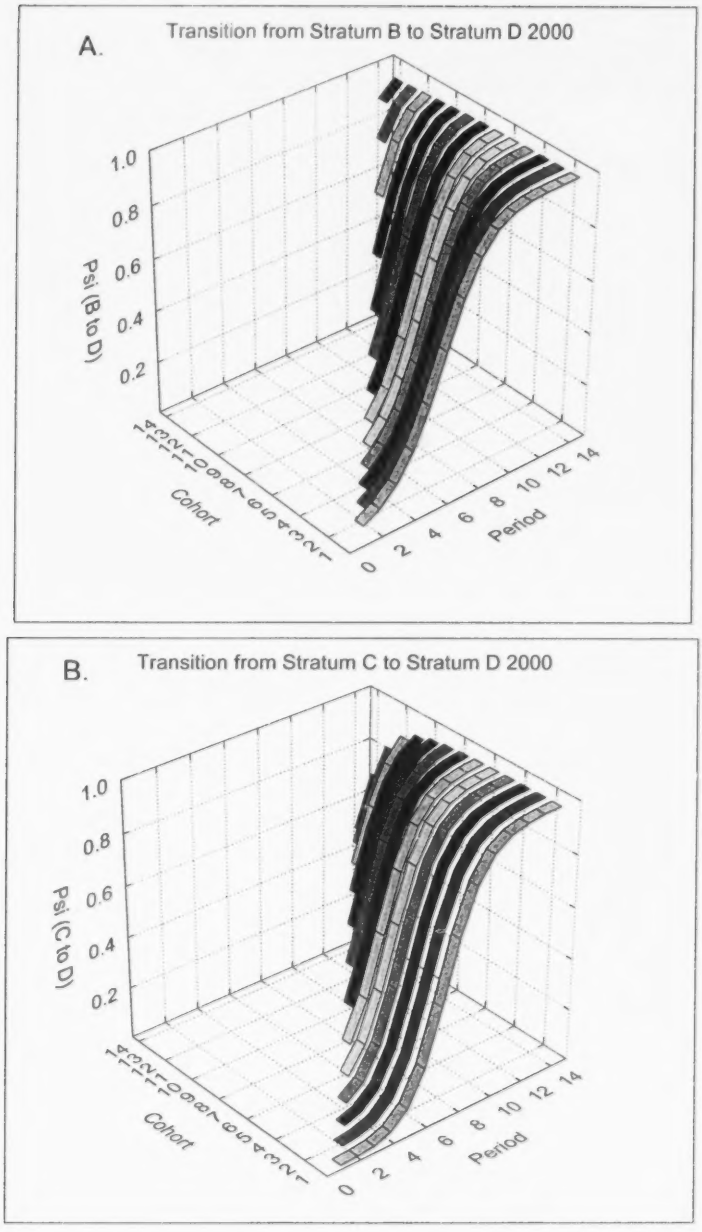


Figure 12. Each graph depicts the transition probability for each cohort of birds, each period, in 2000. A) Transition from Stratum B to D. B) Transition from Stratum C to D. B) Transition from Stratum C to D. The probably of remaining on Stratum B (or C) in a given week *i*, is the complement to this probability 1- Φ_i^{BD} (or 1- Φ_i^{CD}). The arrival and departure weeks are listed in Appendix F.

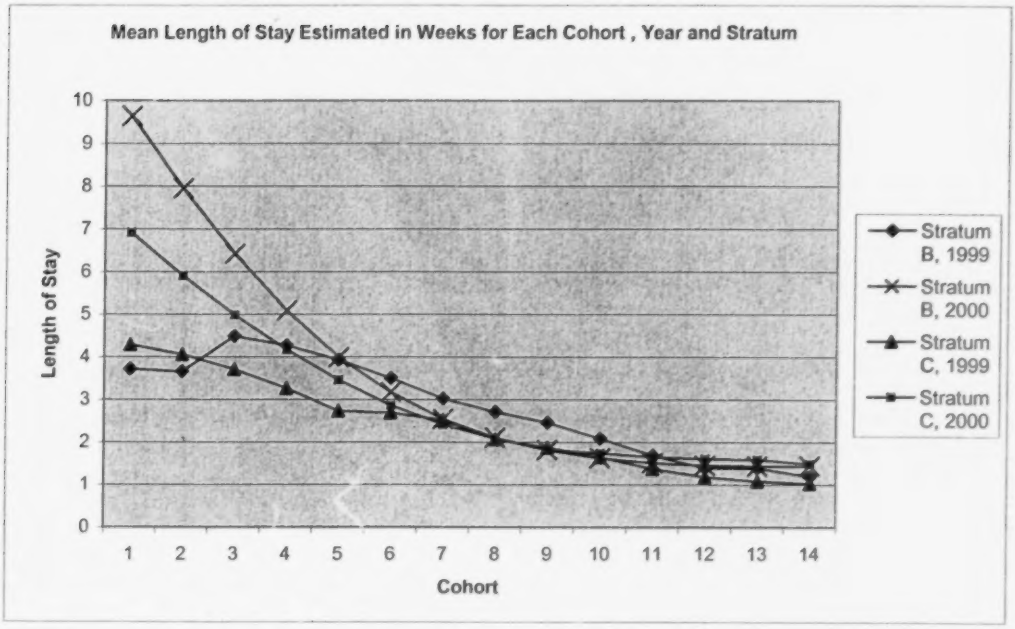


Figure 13. The mean length of stay, estimated in weeks for each cohort, year and stratum.

Table 14. Volume estimates adjusted for three proposed levels of error in abundance counts (5%, 10% and 20%) and three levels of uncertainty among the standard error estimates for transition parameters.

Uncertainty in Transition Parameters	Volume Estimate	Stratum B 1999			Stratum B 2000			Stratum C 1999			Stratum C 2000		
		5%	10%	20%	5%	10%	20%	5%	10%	20%	5%	10%	20%
Underestimate	Total	17562	17641	18040	10421	10858	11119	14025	14111	14356	14727	14828	15072
	S.D.	1437	1587	2069	456	603	982	494	734	1449	980	1170	1731
Intermediate	Total	16783	16876	17242	10645	10685	10898	13838	13921	14210	14242	14304	14603
	S.D.	315	628	1416	195	356	832	299	617	1383	289	619	1309
Overestimate	Total	10987	11037	11206	7460	7492	7710	5388	5420	10841	8135	8150	7940
	S.D.	215	429	912	138	261	594	132	231	1109	167	343	699

Table 15. Volumes estimates as proportions (%) of the Pacific Flyway Brant Population for each abundance error-transition parameter uncertainty combination.

Uncertainty in Transition Parameters	Volume Estimate	Stratum B 1999			Stratum B 2000			Stratum C 1999			Stratum C 2000		
		5%	10%	20%	5%	10%	20%	5%	10%	20%	5%	10%	20%
Underestimate	Total	14.6	14.7	15.0	8.7	9.0	9.3	11.7	11.8	12.0	12.3	12.4	12.6
	S.D.	1.2	1.3	1.7	0.4	0.5	0.8	0.4	0.6	1.2	0.8	1.0	1.4
Intermediate	Total	14.0	14.1	14.4	8.9	8.9	9.1	11.5	11.6	11.8	11.9	11.9	12.2
	S.D.	0.3	0.5	1.2	0.2	0.3	0.7	0.2	0.5	1.2	0.2	0.5	1.1
Overestimate	Total	9.2	9.2	9.3	6.2	6.2	6.4	4.5	4.5	9.0	6.8	6.8	6.6
	S.D.	0.2	0.4	0.8	0.1	0.2	0.5	0.1	0.2	0.9	0.1	0.3	0.6

4.4 Discussion

4.4.1 Band Observations, Counts, and Population Composition

During this study, the timing of migration was similar in both years; however, there was a notable difference between years in the number of Brant staging on the Fraser River delta. In 2000, the counts were much lower on the delta. This was not likely a result of observer bias as counts were consistently lower for all researchers and volunteers, all of whom were experienced at surveying Brant.

During spring migration, the proportion of Brant wearing leg-bands was lower on the Fraser River delta than at Parksville-Qualicum. This was attributed the presence of Grey-bellied Brant on the Fraser River delta. Grey-bellied Brant, which are genotypically and phenotypically distinct from Black Brant (Shields 1990), primarily winter in northern Washington (Reed *et al.* 1989). This group of Brant was not leg-banded at the time of the study and their presence on the Fraser River delta during migration likely caused the band ratio to be low at this site. Grey-bellied Brant were not observed on Vancouver Island.

The acquisition of leg-band observation data depended on accessibility to sites where Brant could be observed out of the water. The Fraser River delta had fewer sites than Parksville-Qualicum for observing Brant. This may have contributed to the relatively low number of leg-bands observed on the Fraser River delta and may also have biased the number of observations classified as single-sight. To what extent this may have occurred is unknown.

4.4.2 Migration and Staging Patterns

Differences were observed in the migration and staging patterns on the Fraser River delta compared to Parksville-Qualicum. Early in migration, Brant from the south were more likely to migrate to Parksville-Qualicum, but as weekly periods increased, Brant were more likely to migrate to the Fraser River delta. This was consistent with the count data that suggested the peak of migration occurred approximately two weeks later on the Fraser River delta than in Parksville-Qualicum each year.

There was little evidence of interchange between the two sites with only 0.5% (82-162 Brant) (1999) and 3% (468-786 Brant) (2000) of the bands observed at both sites. Brant exhibit high philopatry to their spring staging areas (e.g. Raveling 1979, Reed 1997) and the lack of interchange suggests different segments of the Pacific Flyway Brant Population were using specific sites.

4.4.3 Length of Stay

Length of stay for multiple-sight Brant, as estimated by the models, ranged from approximately 1 to 9 weeks, but decreased as the time a cohort first arrived on Stratum B or C progressed. Early in migration, Brant may have experienced less pressure to reach the breeding areas. Although the 2000 model estimated lengths of stay of up to 9 weeks, very few birds likely staged for this long since few birds arrived on these strata this early.

4.4.4 Volume Estimates

The volume estimates provided in this study are minimum estimates. This is largely due to the confidence in the abundance counts, which likely underestimates the total number of Brant present during a period. The two main reasons are that daily counts are minimum estimates of the number of Brant in the survey area and the lack of accuracy in the single-sight turnover rates. Turnover time for some single-sight Brant is likely greater than 1 day. Also, some unknown proportion of single-sight Brant is never seen. These two factors could affect the volume estimates for each weekly period. This uncertainty likely leads to a significant underestimation of the true number of birds staging in the study areas.

This study estimated that between 13-27% of the Pacific Flyway Population staged on the Fraser River delta and Parksville-Qualicum in 1999 and 2000. This range represented the minimum and maximum extremes based on the transition probabilities generated in the models. These study results were based on minimum estimates of abundance and exclude other smaller staging areas on the Strait of Georgia, such as Denman Island, the Seal Islets, and the Trent River Estuary on Vancouver Island. Over one thousand Brant can be observed at each of these sites during the peak of migration (Hagmeier unpubl. data).

To further refine the volume estimates in this study, the extent of overlap between minor and main staging areas must be estimated. The counts at smaller sites cannot be added without this information. Although leg-band observation data are limited at smaller sites, preliminary data suggests Denman Island and Texada Island (Martin and Dove unpubl. data) support Brant, which do not use Parksville-Qualicum or the Fraser River delta. Therefore, the numbers observed at these sites could be added to the Parksville-Qualicum and Fraser River delta estimates to achieve a better estimate of the total number of Brant staging in the entire Strait of Georgia.

Some leg-banded Brant observed in Campbell River were also observed in Parksville-Qualicum and the Fraser River delta (Hagmeier unpubl. data). Although not conclusive, this suggests that some Brant travel only short distances between stopovers in the Strait of Georgia. Therefore,

birds observed north of Parksville-Qualicum should not necessarily be considered as different from ones observed at Parksville-Qualicum.

The volume estimates from this study are comparable to other studies. Routledge *et al.* (1999) estimated approximately 12,100 Brant staged in Parksville-Qualicum during the spring of 1990 and Nygren (1991) estimated that 20% of the Pacific Flyway Brant Population staged in the entire Strait of Georgia, approximately 14,100 of which staged in Parksville-Qualicum. Both of these studies used a mean length of stay to calculate volumes.

Relatively little attention has been given to the Fraser River delta as a spring staging area for Brant, yet the volume estimates in this study suggest that it is just as important as the east coast of Vancouver Island. Moreover, separate groups of Brant use these two major sites in the Strait of Georgia as evidenced by the lack of interchange between the two sites and the absence of Grey-bellied Brant on Vancouver Island.

This method of calculating volume and identifying differences in staging patterns at the two sites has limitations; however, Program MARK and population modeling methodologies are improving. Limitations in this analysis may not be problematic in the future. Currently however, it is important for managers and researchers to recognize that even based on minimum estimates, approximately one quarter (30,000-35,000) of the Pacific Flyway Brant Population may stage in the Strait of Georgia.

5. SUMMARY AND CONCLUSIONS

5.1 Introduction

The Strait of Georgia in British Columbia is an important over-wintering and spring staging area for Brant. Historically, Brant wintered throughout the strait, but they are now largely confined to the Fraser River delta, specifically Boundary Bay and Roberts Bank. The Boundary Bay-Roberts Bank population decreased dramatically over the last century, but rebounded in the last 10 years. In spring, the primary staging areas for spring migrants are the Fraser River delta and Parksville-Qualicum on the east coast of Vancouver Island.

The Strait of Georgia is experiencing tremendous growth in development and urbanization. Because of this, the sustainability of the strait to support wintering and spring staging Brant is an important management concern. With this in mind, I examined the population demographics of the Boundary Bay-Roberts Bank wintering population to understand the factors that are important to its growth and maintenance, recent changes in the local distribution, and the impact

of the Brant hunt in British Columbia on the different wintering segments of the Pacific Flyway Brant Population (Chapter 2). I also studied two aspects of Brant ecology in the Strait of Georgia: 1) time-activity budgets and the impacts of disturbance on Brant wintering on the Fraser River delta (Chapter 3) and 2) the migration patterns and the volume of Brant using the Fraser River delta and Parksville-Qualicum as spring staging areas in the Strait of Georgia (Chapter 4).

5.2 Population Composition and Increase and Distribution of Brant Wintering in Boundary Bay and Roberts Bank

The Boundary Bay-Roberts Bank wintering population grew dramatically in the 1990s, after having been nearly decimated in previous decades. In recent decades, several European Arctic goose populations have experienced similar trends in response to decreased hunting pressure and increases in wintering refuges (e.g. Svalbard Brant Geese) (Madsen *et al.* 1999). Exponential growth models suggested that the Boundary Bay-Roberts Bank population grew at an annual rate of approximately 22-26% between 1993-94 and 1999-2000. This is well above growth rates observed for other recovering goose populations, but mean annual productivity over the same time period was approximately 14%, a rate consistent with other populations. Therefore, unlike other goose populations, productivity alone did not account for the increase. Concurrent with the population growth is the increased presence of Grey-bellied Brant in the wintering population (15-20%). Grey-bellied Brant are geographically, morphologically and genetically distinct from Black Brant (Shields 1990). The traditional wintering area of Grey-Bellied Brant is in northern Washington State, 60km south of the Fraser River delta. Grey-bellied have expanded their northern range to include the Fraser River delta.

During this study, Brant wintering on the Fraser River delta expanded their local winter range to include Roberts Bank. Distinct segments of the population seemed to favour one site over the other. Significantly higher proportions of Grey-bellied Brant were observed at Boundary Bay compared to Roberts Bank and significantly higher proportions of juveniles were observed at Roberts Bank compared to Boundary Bay. Leg-band observation data of Black Brant showed there was similar mixing of birds from different breeding grounds at each site, consistent with previous research conducted in this area (Reed 1997).

5.3 Harvest

Evidence from this study suggests that during the British Columbia Brant hunt approximately 70% (105-140) of the harvested Brant are from the Boundary Bay-Roberts Bank wintering population. Less than 1% of Brant from each of the wintering areas south of the Fraser River delta are harvested in the British Columbia season. This, of course, depends on the timing of arrival of migrants from more southern wintering areas into Boundary Bay and Roberts Bank and the number of Brant harvested each year.

5.4 Activity Budgets and Effects of Disturbance

During the day, Brant spent up to 10% of their time responding to disturbance. In Boundary Bay (2000) this was equivalent to almost half of their daily energy expenditure. There were fewer disturbances at Roberts Bank than Boundary Bay, which may be contributing to the increasing use of Roberts Bank as documented in Chapter 2.

During this study, disturbance caused by humans resulted in only 5% of the daily energy expenditure of Brant. Most disturbance events were from natural sources, particularly Bald Eagles. The frequencies of disturbance were 2.17/h and 1.32/h at Boundary Bay and Roberts Bank respectively. High levels of disturbance (>2/h) have been shown to lead to abandonment of wintering areas by Arctic-nesting geese even if they engaged in compensatory nocturnal feeding (Bélanger and Bédard 1990). The increase in the Bald Eagle numbers and the effect on the Brant DEE will ultimately negatively impact Brant remaining in the area.

5.5 Spring Migration Patterns and Volume Estimates

This study identified differences in migration patterns of Brant using the Fraser River delta and the east coast of Vancouver Island. Each site is an important staging area and is used by a separate component of the Pacific Flyway Brant Population. This is to be expected as Arctic-nesting geese exhibit high philopatry to staging and nesting areas and high philopatry has been observed in spring staging Brant at Parksville-Qualicum (Reed 1997).

This study estimated that between 13-27% of the Pacific Flyway Population stages on the Fraser River delta and Parksville-Qualicum. This is a minimum estimate and suggests that these are critical staging areas for the Pacific Flyway Brant Population.

5.6 Research and Management Implications

The results of this research have considerable management implications, a primary one being that the Boundary Bay-Roberts Bank wintering population cannot be effectively managed in

isolation. Although the wintering population may be closed within a year (Reed 1997), across years, immigration of Brant from Washington State affects the size of the population. Furthermore, immigration likely contains both Black and Grey-bellied Brant, but it is only the morphologically distinct Grey-bellied Brant that can be identified as a specifically increasing component of the wintering population. Continued and increased effort with Washington State for management of wintering Brant as a trans-boundary unit will undoubtedly yield the most successful management results.

Because the causes of disturbance in most studies of Arctic-nesting geese are human-related, management problems in those situations can be fairly easily resolved (e.g. changing aircraft flight paths or hunting boundaries); however in this study the causes of disturbance were primarily from Bald Eagles. Therefore, management of disturbance will be challenging. I suggest that it may be critical to maintain or decrease the current levels human disturbance, should the Brant be approaching a threshold that would force them to abandon this wintering area.

The information presented in this thesis is important for current management planning; however also provides a baseline for future research which may answer some critical questions about the Pacific Flyway Brant Population, for example,

- Correlating the probability of arrival to staging areas and lengths of stay with respect to resource availability (e.g. timing and abundance of herring spawn),
- Determining which components of the Pacific Flyway Brant Population are staging on the Fraser River delta and Vancouver Island. Currently, the amount of data on Brant migrating through the Strait of Georgia and their reproductive fates is limited, but as this data set increases, the importance of the Strait of Georgia in terms of nutrient accumulation of breeding Brant could be quantified and used as a tool in the conservation and management,
- Understanding the population dynamics of Grey-bellied Brant.

It seems essential that the Pacific Flyway Brant Population be researched on a flyway-wide scale and that the connectivity between different projects be increased. Therefore, decisions made by regional biologists and managers will consider the impacts all along the Flyway, and through adaptive management, our capability to manage and conserve this population will continue to improve.

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Appendix A

Calculations for Harvest Estimates using Leg-band Data

1. Assumed 8-10% of the Pacific Flyway Brant Population (PFBP) is banded and equally distributed along the Flyway
   - Based on observations from Boundary Bay, Roberts Bank, Vancouver Island, Oregon and California.

2. Removed Grey-bellied Brant from analysis
   - Grey-bellied Brant were not banded at the time of this study

3. Estimated 3-year population means for each wintering area (Subcommittee on Pacific Brant 2001).

Table 16. 3-year population means for each wintering area on the Pacific Flyway

	Year				
Site	**1997-98**	**1998-99**	**1999-00**	**Mean**	**SD**
BC	619	985	1238	947	311
WA	4541	6037	5944	5507	838
OR	580	645	523	583	61
CA	6091	4296	3389	4592	1375
MEX	112105	100760	108440	107102	5790

BC = British Columbia, WA = Washington, OR = Oregon, CA = California, MEX = Mexico.

4. Pooled the band data from 10 days before and 10 days of the hunt to establish which segments of the PFBP were vulnerable to hunting and estimated the proportion of birds from each wintering area present in Boundary Bay and Roberts Bank before and during the hunt using the leg-band data.

Table 17. The number of leg bands observed in Boundary Bay and Roberts Bank from each of the wintering areas.

	Year				
Site	**1997-98**	**1998-99**	**1999-00**	**Total**	**Proportion of Population (%)**
10 days before					
BC	15	7	31	53	*
WA	0	0	0	0	*
OR	0	0	0	0	*
CA	4	0	0	4	*
MEX	11	1	1	13	*
10 days of hunt					
BC	13	10	14	37	*
WA	0	0	3	3	*
OR	0	0	0	0	*
CA	2	0	0	2	*
MEX	11	3	2	16	*
Total					
BC	28	17	45	90	70.3
WA	0	0	3	3	2.3
OR	0	0	0	0	0.0
CA	6	0	0	6	4.7
MEX	22	4	3	29	22.7

BC = British Columbia, WA = Washington, OR = Oregon, CA = California, MEX = Mexico.

5. Estimated the number of birds harvested from each wintering ground based on a total harvest of 150-200 Brant.

Table 18. Estimated number of Brant shot in Boundary Bay-Roberts Bank.

Wintering area	Estimated # Brant shot
BC	**105-140**
WA	**3-5**
OR	**0**
CA	**7-9**
MEX	**34-45**

6. Estimated the proportion of birds harvested from each wintering population by dividing the estimate of birds harvested from each wintering area (Step 5) by the mean wintering population size of each area (Step 3). The harvested proportions from each wintering population were BC = 11-15%, Washington < 1%, Oregon < 1%, California < 1%, and Mexico < 1%.

Appendix B

Effects of Bald Eagle and Human Population Growth on DEE of Brant in Boundary Bay.

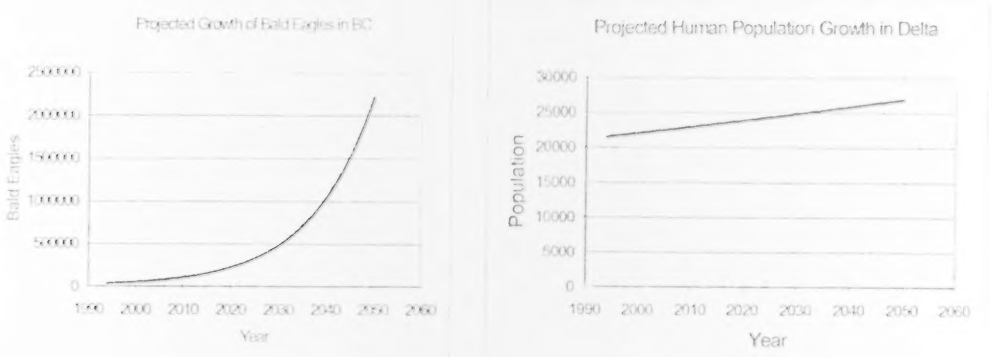


Figure 14. The predicted sizes of the BC Coastal Bald Eagle population and the human population of Delta. In 1994 there were 30 000 Bald Eagles, increasing at an annual rate of 8% (CWS unpubl. data). The human population of Delta is increasing by 0.4% each year (Corportation of Delta, Department of Community Planning and Development).

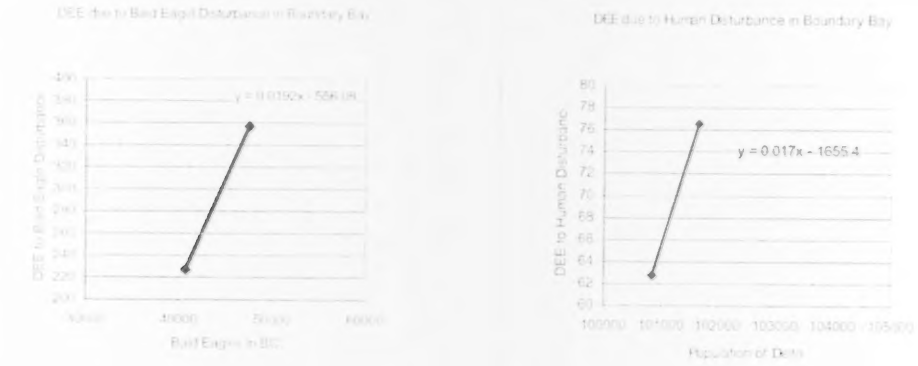
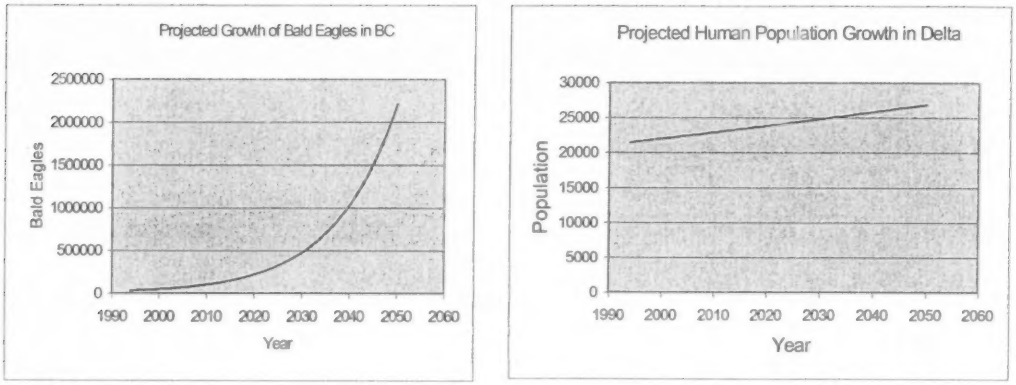


Figure 15. The relationship between Bald Eagles and DEE and between people and DEE using the two years of data from Boundary Bay.

Appendix B

Effects of Bald Eagle and Human Population Growth on DEE of Brant in Boundary Bay.



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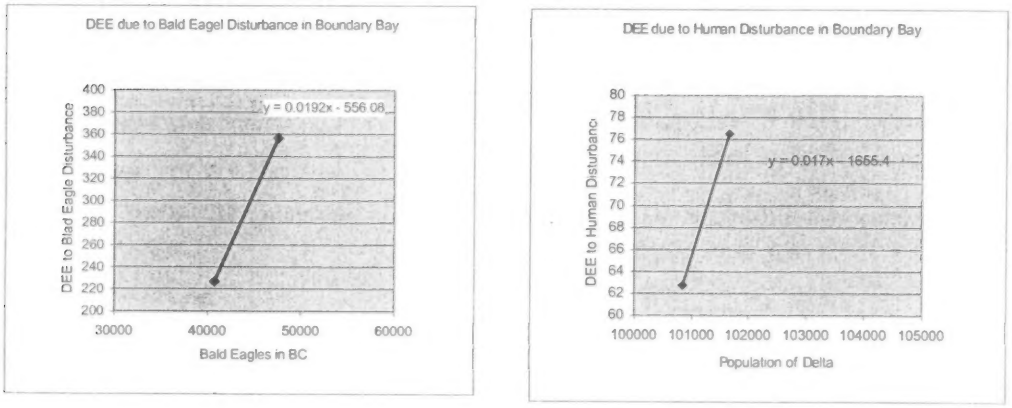


Figure 15. The relationship between Bald Eagles and DEE and between people and DEE using the two years of data from Boundary Bay.

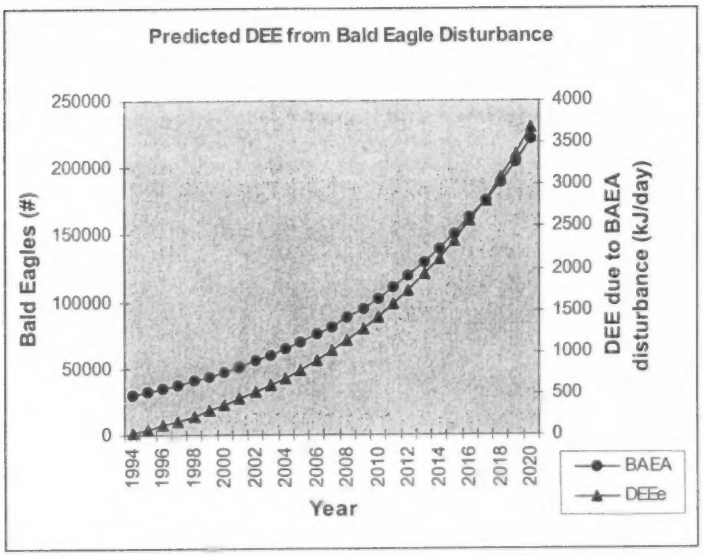


Figure 16. The predicted growth of the Bald Eagle population in BC and the associated increase in Brant DEE due to Bald Eagle disturbance (DEEe).

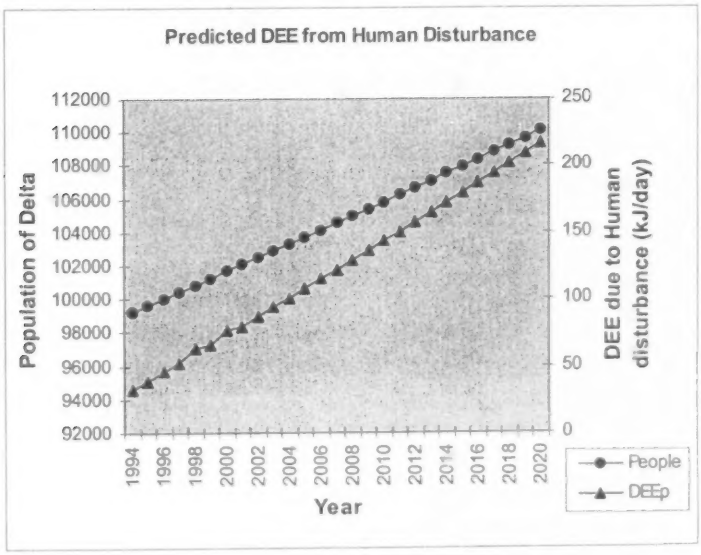


Figure 17. The predicted growth of the human population in Delta, BC and the associated increase in DEE due to human disturbance (DEEp).

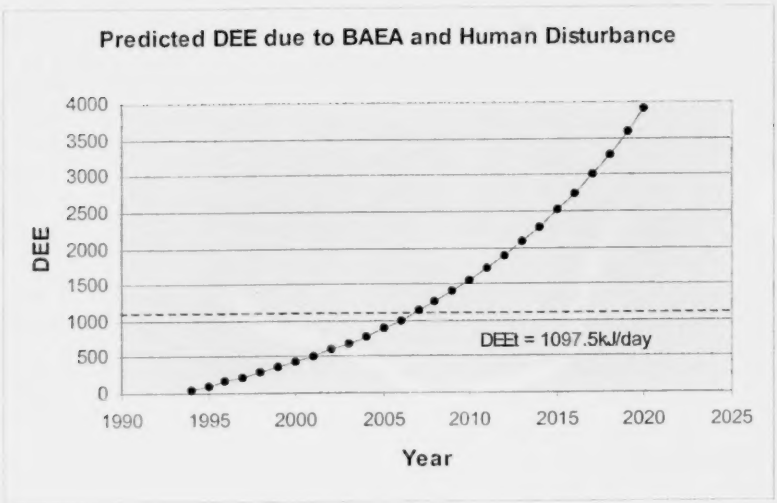


Figure 18. The predicted DEE caused by human and Bald Eagle disturbances. Using 1097.5 Kj/day as the DEEt guideline, by 2007 all energy would be expended responding to disturbance.

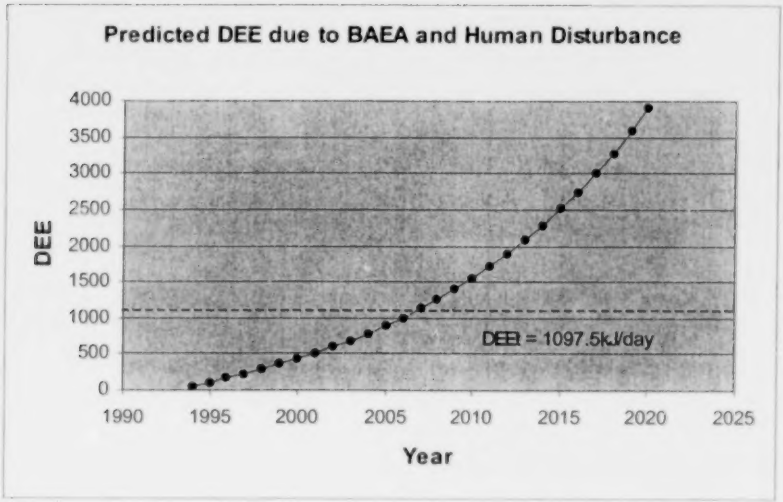


Figure 18. The predicted DEE caused by human and Bald Eagle disturbances. Using 1097.5 Kj/day as the DEEt guideline, by 2007 all energy would be expended responding to disturbance

Appendix C.

Frequency Distribution of Leg-Band Observations

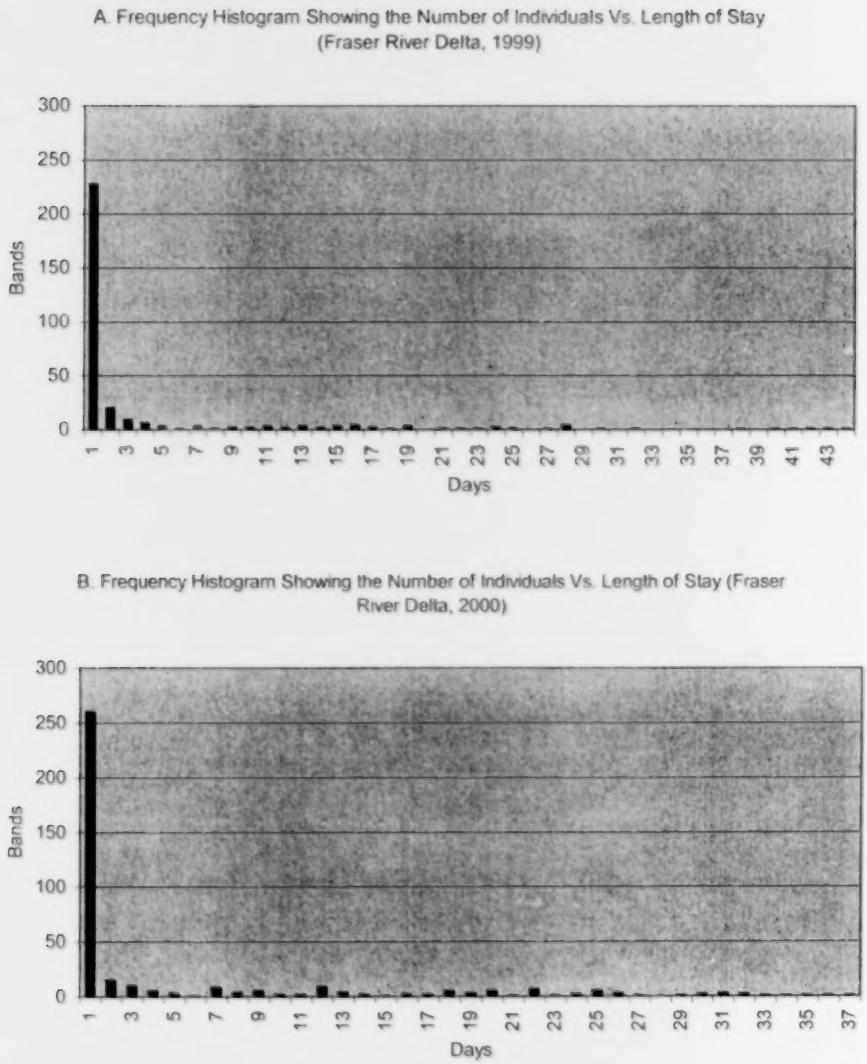
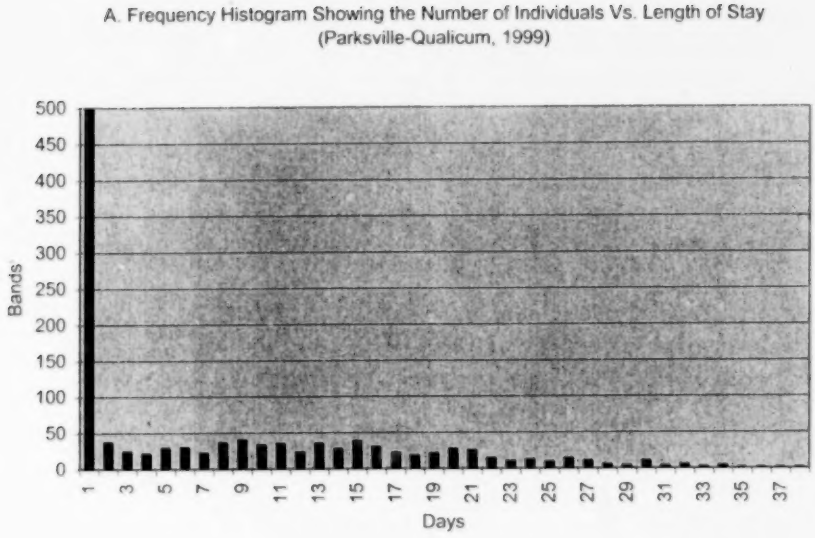

A. Frequency Histogram Showing the Number of Individuals Vs. Length of Stay (Fraser River Delta, 1999)
Bands
Days
B. Frequency Histogram Showing the Number of Individuals Vs. Length of Stay (Fraser River Delta, 2000)
Bands
Days

Figure 19. Frequency distribution of length of stay (first and last days a band was observed) on A) Fraser River Delta 1999 and B) Fraser River Delta 2000.



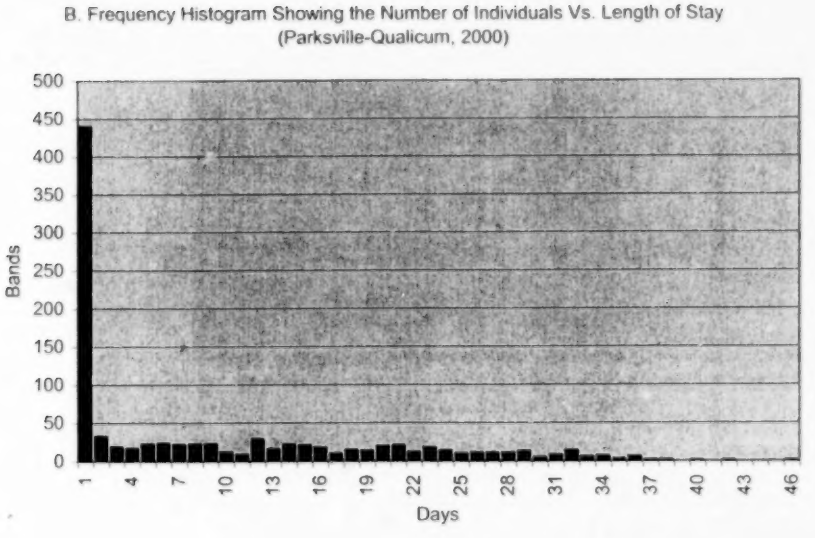


Figure 20. Frequency distribution of length of stay (first and last days a band was observed in A) Parksville-Qualicum 1999 and B) Parksville-Qualicum 2000.

Appendix D.

Lengths of Stay for Individually Leg-Banded Brant Observed in 1999 and 2000.

Data exploration suggested that individual Brant staged for similar lengths of time across years (Figure 21).

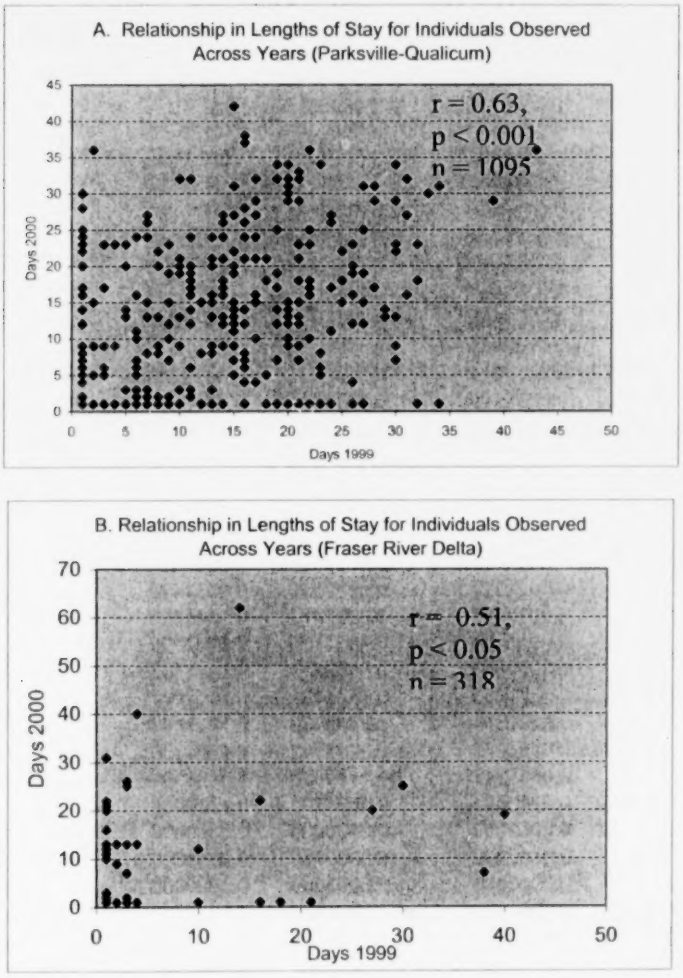


Figure 21. The relationship between lengths of stay for individually banded Brant observed in consecutive years at A) Parksville-Qualicum ($r = 0.63$, $p < 0.001$, $n = 1095$) and B) the Fraser River delta ($r = 0.51$, $p = 0.05$, $n = 318$). Each axis represents the number of days an individual Brant staged at a site, each year, based on the first and the last days a band was observed.

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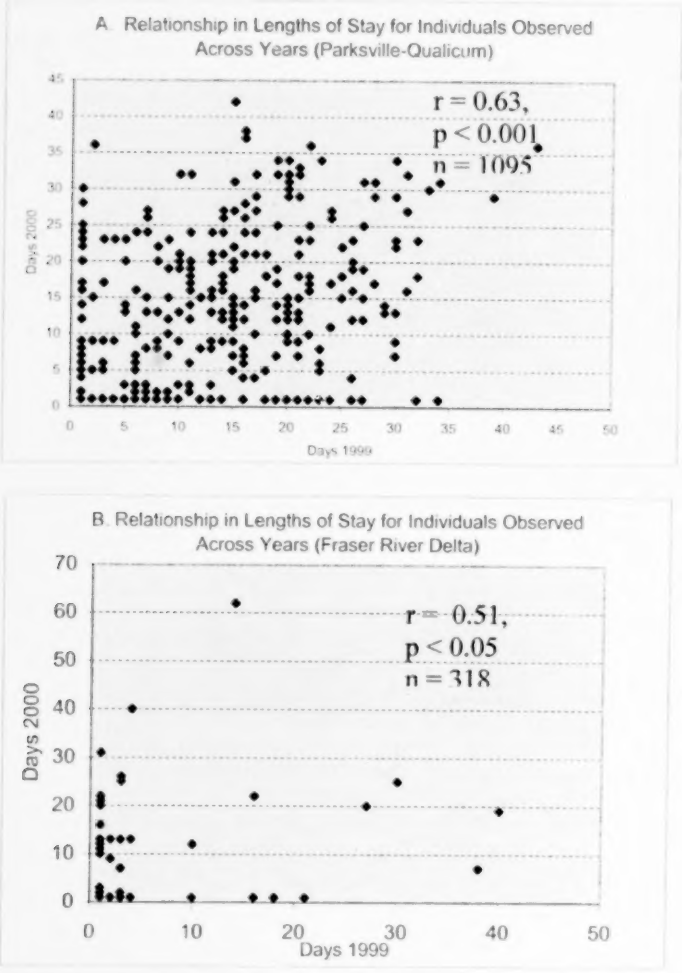
A. Relationship in Lengths of Stay for Individuals Observed Across Years (Parksville-Qualicum)
r = 0.63,
p < 0.001
n = 1095
Days 2000
Days 1999
B. Relationship in Lengths of Stay for Individuals Observed Across Years (Fraser River Delta)
r = 0.51,
p < 0.05
n = 318
Days 2000
Days 1999

Figure 21. The relationship between lengths of stay for individually banded Brant observed in consecutive years at A) Parksville-Qualicum ($r = 0.63$, $p < 0.001$, $n = 1095$) and B) the Fraser River delta ($r = 0.51$, $p = 0.05$, $n = 318$). Each axis represents the number of days an individual Brant staged at a site, each year, based on the first and the last days a band was observed.

Appendix E.

Transition Probabilities

Table 19. Single Sight Transitions Probabilities from A to B and A to C. Parameters 4-30 are 1999 and 31-59 are 2000.

			95% Confidence Interval	
Parameter	Estimate	Standard Error	Lower	Upper
1:S A:South	1.0000000	0.0000000	1.0000000	1.0000000
2:p A:South	1.0000000	0.0000000	1.0000000	1.0000000
3:Psi B to A	0.0000000	0.0000000	0.0000000	0.0000000
4:Psi A to B	0.0076753	0.0023437	0.0042137	0.0139406
5:Psi A to B	0.0087745	0.0018933	0.0057445	0.0133812
6:Psi A to B	0.0109857	0.0016972	0.0081119	0.0148624
7:Psi A to B	0.0150517	0.0018440	0.0118338	0.0191276
8:Psi A to B	0.0225313	0.0025108	0.0181012	0.0280148
9:Psi A to B	0.0367211	0.0038828	0.0298247	0.0451378
10:Psi A to B	0.0646522	0.0061565	0.0535837	0.0778191
11:Psi A to B	0.1208111	0.0097065	0.1030407	0.1411639
12:Psi A to B	0.2304773	0.0169049	0.1990190	0.2652613
13:Psi A to B	0.4171616	0.0329011	0.3544211	0.4827041
14:Psi A to B	0.6522114	0.0478199	0.5536855	0.7392308
15:Psi A to B	0.8434351	0.0414580	0.7443435	0.9088238
16:Psi A to B	0.9443429	0.0231755	0.8772925	0.9757673
17:Psi A to B	0.0000000	0.0000000	0.0000000	0.0000000
18:Psi A to B	0.0000000	0.0000000	0.0000000	0.0000000
19:Psi A to B	0.0063544	0.0020156	0.0034089	0.0118146
20:Psi A to B	0.0114731	0.0023774	0.0076372	0.0172024
21:Psi A to B	0.0205537	0.0027782	0.0157593	0.0267670
22:Psi A to B	0.0364231	0.0037485	0.0297481	0.0445270
23:Psi A to B	0.0635233	0.0060104	0.0527126	0.0763724
24:Psi A to B	0.1081527	0.0094667	0.0909479	0.1281533
25:Psi A to B	0.1776209	0.0137555	0.1522422	0.2062011
26:Psi A to B	0.2770556	0.0220363	0.2359972	0.3222443
27:Psi A to B	0.4038512	0.0406682	0.3272772	0.4854136
28:Psi A to B	0.5440011	0.0667247	0.4132020	0.6690000
29:Psi A to B	0.6766897	0.0882623	0.4869732	0.8219068
30:Psi A to B	0.0000000	0.0000000	0.0000000	0.0000000
31:Psi A to B	0.0000000	0.0000000	0.0000000	0.0000000
32:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000
33:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000
34:Psi A to C	0.0088932	0.0021410	0.0055432	0.0142390
35:Psi A to C	0.0338747	0.0045555	0.0259967	0.0440322
36:Psi A to C	0.0925354	0.0067953	0.0800497	0.1067427
37:Psi A to C	0.1808132	0.0101094	0.1618373	0.2014793
38:Psi A to C	0.2623136	0.0134250	0.2368625	0.2894622
39:Psi A to C	0.2989183	0.0149620	0.2704405	0.3290424
40:Psi A to C	0.2756233	0.0205254	0.2372579	0.3176093
41:Psi A to C	0.2017416	0.0293701	0.1502170	0.2654193
42:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000
43:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000
44:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000

Table 19 Continued.

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
45:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000
46:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000
47:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000
48:Psi A to C	0.0295051	0.0049265	0.0212388	0.0408544
49:Psi A to C	0.0667803	0.0061635	0.0556678	0.0799235
50:Psi A to C	0.1249149	0.0077036	0.1105812	0.1408124
51:Psi A to C	0.1944088	0.0111445	0.1734911	0.2171859
52:Psi A to C	0.2569263	0.0138452	0.2307386	0.2849850
53:Psi A to C	0.2956983	0.0161588	0.2650386	0.3283203
54:Psi A to C	0.3017040	0.0241071	0.2566466	0.3509373
55:Psi A to C	0.2736873	0.0384968	0.2049606	0.3551643
56:Psi A to C	0.2178465	0.0526729	0.1319117	0.3379685
57:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000
58:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000
59:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000

Table 20. Multiple-Sight Transitions Probabilities from A to B and A to C, 1999.

Parameter	Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:S A:South	1.0000000	0.0000000	1.0000000	1.0000000
2:p A:South	1.0000000	0.0000000	1.0000000	1.0000000
3:Psi B to A	0.0000000	0.0000000	0.0000000	0.0000000
4:Psi A to B	0.0056686	0.0025070	0.0023785	0.0134484
5:Psi A to B	0.0000000	0.0000000	0.0000000	0.0000000
6:Psi A to B	0.0048935	0.0011902	0.0030365	0.0078772
7:Psi A to B	0.0000000	0.0000000	0.0000000	0.0000000
8:Psi A to B	0.0094019	0.0018472	0.0063931	0.0138072
9:Psi A to B	0.0175222	0.0031606	0.0122919	0.0249221
10:Psi A to B	0.0393741	0.0060163	0.0291352	0.0530147
11:Psi A to B	0.1033071	0.0128682	0.0806701	0.1313885
12:Psi A to B	0.2836972	0.0343119	0.2214674	0.3554299
13:Psi A to B	0.6247965	0.0635073	0.4947458	0.7390299
14:Psi A to B	0.8954304	0.0399489	0.7877181	0.9518313
15:Psi A to B	0.9817700	0.0111792	0.9405896	0.9945709
16:Psi A to B	0.9975918	0.0020682	0.9871204	0.9995536
17:Psi A to B	0.9997435	0.2908E-03	0.9976368	0.9999722
18:Psi A to C	0.5860E-03	0.2382E-03	0.2641E-03	0.0012997
19:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000
20:Psi A to C	0.0286803	0.0041660	0.0215508	0.0380766
21:Psi A to C	0.1069731	0.0075425	0.0930635	0.1226805
22:Psi A to C	0.2507931	0.0107437	0.2303285	0.2724323
23:Psi A to C	0.3918625	0.0145869	0.3636716	0.4207935
24:Psi A to C	0.4607439	0.0165285	0.4285584	0.4932602
25:Psi A to C	0.4383255	0.0227628	0.3943225	0.4833204
26:Psi A to C	0.3293054	0.0355050	0.2637808	0.4022143
27:Psi A to C	0.1754548	0.0389583	0.1115248	0.2650971
28:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000
29:Psi A to C	0.0128947	0.0075439	0.0040717	0.0400669
30:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000
31:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000

Table 21. Multiple-Sight Transitions Probabilities from B to D and C to D, 1999.

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:S B:BB	1.0000000	0.0000000	1.0000000	1.0000000
2:p D:North	1.0000000	0.0000000	1.0000000	1.0000000
3:Psi D to B	0.0000000	0.0000000	0.0000000	0.0000000
4:p B:BB	0.0000000	0.0000000	0.0000000	0.0000000
5:p B:BB	0.6666658	0.2721615	0.1535119	0.9566281
6:p B:BB	0.4999970	0.3535508	0.0588644	0.9411343
7:p B:BB	0.4000008	0.2190885	0.1002289	0.7995942
8:p B:BB	0.4920114	0.2042714	0.1633032	0.8277750
9:p B:BB	0.0901113	0.0859984	0.0125171	0.4362278
10:p B:BB	0.7807219	0.1197499	0.4747393	0.9334470
11:p B:BB	0.0454544	0.0444092	0.0063644	0.2614575
12:p B:BB	0.8461535	0.0707588	0.6546128	0.9410393
13:p B:BB	0.6842096	0.1066385	0.4516117	0.8507546
14:p B:BB	0.9642854	0.0350708	0.7858133	0.9949924
15:p B:BB	1.0000000	0.0000000	1.0000000	1.0000000
16:p B:BB	1.0000000	0.0000000	1.0000000	1.0000000
17:p B:BB	0.0000000	0.0000000	0.0000000	0.0000000
18:p C:PQ	0.0000000	0.0000000	0.0000000	0.0000000
19:p C:PQ	0.6666678	0.2721617	0.1535119	0.9566289
20:p C:PQ	0.3333346	0.2721635	0.0433712	0.8464905
21:p C:PQ	0.6363638	0.1450404	0.3387485	0.8566953
22:p C:PQ	0.6152076	0.0497300	0.5143743	0.7070292
23:p C:PQ	0.8028497	0.0258188	0.7473423	0.8486324
24:p C:PQ	0.9003335	0.0153500	0.8659546	0.9266422
25:p C:PQ	0.9135338	0.0172324	0.8732467	0.9418686
26:p C:PQ	0.9083334	0.0263413	0.8420271	0.9485107
27:p C:PQ	1.0000000	0.0000000	1.0000000	1.0000000
28:p C:PQ	0.0000000	0.0000000	0.0000000	0.0000000
29:p C:PQ	0.0000000	0.0000000	0.0000000	0.0000000
30:p C:PQ	0.0000000	0.0000000	0.0000000	0.0000000
31:p C:PQ	0.0000000	0.0000000	0.0000000	0.0000000
32:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
33:Psi B to C	0.2211473	0.1934258	0.0304702	0.7195187
34:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
35:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
36:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
37:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
38:Psi B to C	0.0744050	0.0706254	0.0106562	0.3749773
39:Psi B to C	0.0928602	0.0544454	0.0280308	0.2665133
40:Psi B to C	0.0263191	0.0258673	0.0037240	0.1635068
41:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
42:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
43:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
44:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
45:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
46:Psi B to D	0.1516422	0.1764692	0.0120047	0.7244850
47:Psi B to D	0.1544299	0.1357127	0.0232644	0.5834009
48:Psi B to D	0.1700413	0.1190211	0.0377488	0.5169065
49:Psi B to D	0.2014959	0.1285200	0.0500883	0.5470203
50:Psi B to D	0.2544193	0.1638867	0.0590468	0.6498098

Table 21 Continued.

Parameter	Estimate	Standard Error	95% Confidence Interval Lower	95% Confidence Interval Upper
51:Psi B to D	0.3362700	0.2169983	0.0700732	0.7730552
52:Psi B to D	0.4523167	0.2675238	0.0904665	0.8727308
53:Psi B to D	0.5964655	0.2810995	0.1303052	0.9358230
54:Psi B to D	0.7438853	0.2345681	0.2063793	0.9700963
55:Psi B to D	0.8623789	0.1511694	0.3404387	0.9870256
56:Psi B to D	0.9368818	0.0772576	0.5341599	0.9948225
57:Psi B to D	0.9747494	0.0331630	0.7335031	0.9981564
58:Psi B to D	0.9910094	0.0126541	0.8720097	0.9994396
59:Psi B to D	0.9971145	0.0044609	0.9430148	0.9998614
60:Psi B to D	0.1154082	0.1083837	0.0160242	0.5110474
61:Psi B to D	0.1276704	0.0854586	0.0315021	0.3970579
62:Psi B to D	0.1527295	0.0786662	0.0519135	0.3724228
63:Psi B to D	0.1959880	0.0939298	0.0704436	0.4394915
64:Psi B to D	0.2657406	0.1316037	0.0880005	0.5758142
65:Psi B to D	0.3710546	0.1807737	0.1144637	0.7291956
66:Psi B to D	0.5135914	0.2156651	0.1627802	0.8515037
67:Psi B to D	0.6747791	0.2044773	0.2504201	0.9279845
68:Psi B to D	0.8173969	0.1469353	0.3939656	0.9685772
69:Psi B to D	0.9138178	0.0815153	0.5823592	0.9877496
70:Psi B to D	0.9650058	0.0373156	0.7597189	0.9958594
71:Psi B to D	0.9874594	0.0151020	0.8782387	0.9988380
72:Psi B to D	0.9959654	0.0056286	0.9406643	0.9997399
73:Psi B to D	0.0957584	0.0699236	0.0212891	0.3401793
74:Psi B to D	0.1153823	0.0566413	0.0421052	0.2790374
75:Psi B to D	0.1499347	0.0552805	0.0700958	0.2921414
76:Psi B to D	0.2075275	0.0738157	0.0980028	0.3869447
77:Psi B to D	0.2991712	0.1108794	0.1314999	0.5461846
78:Psi B to D	0.4331100	0.1508247	0.1864586	0.7180563
79:Psi B to D	0.6002071	0.1648610	0.2808460	0.8523214
80:Psi B to D	0.7640940	0.1353776	0.4263462	0.9338437
81:Psi B to D	0.8846902	0.0839203	0.6047368	0.9746670
82:Psi B to D	0.9522750	0.0420537	0.7649037	0.9918943
83:Psi B to D	0.9827512	0.0183483	0.8722595	0.9979009
84:Psi B to D	0.9944326	0.0072500	0.9320490	0.9995703
85:Psi B to D	0.0872545	0.0486537	0.0280582	0.2404451
86:Psi B to D	0.1144737	0.0411571	0.0551162	0.2226905
87:Psi B to D	0.1610254	0.0437593	0.0923322	0.2658559
88:Psi B to D	0.2383092	0.0642145	0.1352461	0.3849489
89:Psi B to D	0.3589561	0.0976637	0.1959540	0.5626640
90:Psi B to D	0.5238828	0.1240612	0.2933311	0.7446859
91:Psi B to D	0.7036070	0.1193048	0.4361626	0.8793000
92:Psi B to D	0.8490142	0.0853300	0.6040101	0.9539805
93:Psi B to D	0.9359966	0.0479637	0.7527677	0.9859630
94:Psi B to D	0.9766125	0.0227272	0.8558960	0.9966054
95:Psi B to D	0.9924192	0.0094636	0.9175150	0.9993514
96:Psi B to D	0.0875652	0.0376574	0.0367023	0.1946705
97:Psi B to D	0.1247155	0.0348539	0.0708096	0.2103678
98:Psi B to D	0.1884876	0.0413620	0.1202703	0.2829526
99:Psi B to D	0.2936352	0.0623210	0.1874433	0.4282786
100:Psi B to D	0.4495988	0.0895370	0.2866995	0.6240758

Table 21 Continued.

Parameter	Estimate	Standard Error	95% Confidence Interval Lower	Upper
101:Psi B to D	0.6379869	0.1020988	0.4256046	0.8073811
102:Psi B to D	0.8067446	0.0863946	0.5848903	0.9251942
103:Psi B to D	0.9156593	0.0552616	0.7275568	0.9778452
104:Psi B to D	0.9687501	0.0283891	0.8314560	0.9948929
105:Psi B to D	0.9898153	0.0123511	0.8980058	0.9990687
106:Psi B to D	0.0967751	0.0333784	0.0482443	0.1846534
107:Psi B to D	0.1486871	0.0350950	0.0920917	0.2312064
108:Psi B to	7381478	0.0448353	0.1614863	0.3365934
109:Psi B to	05158	0.0649423	0.2635994	0.5131531
110:Psi B to D	9311	0.0855302	0.4007440	0.7242228
111:Psi B to D	83999	0.0863194	0.5549204	0.8876823
112:Psi B to D	08751	0.0631973	0.6954197	0.9668770
113:Psi B to D	88663	0.0351183	0.8027816	0.9925649
114:Psi B to D	0.9865012	0.0158936	0.8756941	0.9986827
115:Psi B to D	0.1174114	0.0337896	0.0656031	0.2013189
116:Psi B to D	0.1923052	0.0388075	0.1273268	0.2798114
117:Psi B to D	0.3187333	0.0496427	0.2301099	0.4227468
118:Psi B to D	0.5023326	0.0690265	0.3700857	0.6342538
119:Psi B to D	0.7050967	0.0825531	0.5233683	0.8388685
120:Psi B to D	0.8614603	0.0698543	0.6637992	0.9514167
121:Psi B to D	0.9466818	0.0422367	0.7749720	0.9891938
122:Psi B to D	0.9823520	0.0199364	0.8538848	0.9981175
123:Psi B to D	0.1551834	0.0372938	0.0951716	0.2428789
124:Psi B to D	0.2652202	0.0420588	0.1912330	0.3552589
125:Psi B to D	0.4378036	0.0524489	0.3390023	0.5417976
126:Psi B to D	0.6484599	0.0723359	0.4975828	0.7745566
127:Psi B to D	0.8275070	0.0725866	0.6390745	0.9285597
128:Psi B to D	0.9319650	0.0486287	0.7528875	0.9840226
129:Psi B to D	0.9772441	0.0241714	0.8361026	0.9972415
130:Psi B to D	0.2200126	0.0427454	0.1475676	0.3148850
131:Psi B to D	0.3783250	0.0423897	0.2994499	0.4642091
132:Psi B to D	0.5904179	0.0563806	0.4771973	0.6948008
133:Psi B to D	0.7894275	0.0693086	0.6234636	0.8946062
134:Psi B to D	0.9145648	0.0529940	0.7391132	0.9758734
135:Psi B to D	0.9710647	0.0281651	0.8247196	0.9958397
136:Psi B to D	0.3251029	0.0525258	0.2315407	0.4350675
137:Psi B to D	0.5329369	0.0488182	0.4372170	0.6262919
138:Psi B to D	0.7479527	0.0619970	0.6090099	0.8497056
139:Psi B to D	0.8944416	0.0546823	0.7314069	0.9634591
140:Psi B to D	0.9637214	0.0315101	0.8195217	0.9936064
141:Psi B to D	0.4777677	0.0746437	0.3372990	0.6218430
142:Psi B to D	0.7040787	0.0652317	0.5629521	0.8146393
143:Psi B to D	0.8716927	0.0560342	0.7178956	0.9477461
144:Psi B to D	0.9551545	0.0342782	0.8161025	0.9903120
145:Psi B to D	0.6589679	0.0996388	0.4476148	0.8216709
146:Psi B to D	0.8465651	0.0662109	0.6701425	0.9374380
147:Psi B to D	0.9453471	0.0380473	0.8033217	0.9865325
148:Psi B to D	0.8194522	0.0972072	0.5559816	0.9426981
149:Psi B to D	0.9343357	0.0470354	0.7599968	0.9846005
150:Psi B to D	0.9222157	0.0666441	0.6574409	0.9865305

Table 21 Continued.

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
151:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
152:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
153:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
154:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
155:Psi C to B	0.0110883	0.0110602	0.0015504	0.0748997
156:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
157:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
158:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
159:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
160:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
161:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
162:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
163:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
164:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
165:Psi C to D	0.926E-04	0.175E-03	0.226E-05	0.0037787
166:Psi C to D	0.139E-03	0.197E-03	0.862E-05	0.0022462
167:Psi C to D	0.251E-03	0.270E-03	0.306E-04	0.0020672
168:Psi C to D	0.546E-03	0.478E-03	0.981E-04	0.0030386
169:Psi C to D	0.0014256	0.0011533	0.291E-03	0.0069373
170:Psi C to D	0.0044566	0.0036345	0.897E-03	0.0218105
171:Psi C to D	0.0165866	0.0137286	0.0032299	0.0807061
172:Psi C to D	0.0709399	0.0555487	0.0144247	0.2848773
173:Psi C to D	0.2934636	0.1690703	0.0774982	0.6725172
174:Psi C to D	0.7308077	0.1531164	0.3712694	0.9258227
175:Psi C to D	0.9551993	0.0334944	0.8213630	0.9899868
176:Psi C to D	0.9950544	0.0044315	0.9717857	0.9991499
177:Psi C to D	0.9995619	0.512E-03	0.9956651	0.9999559
178:Psi C to D	0.9999678	0.510E-04	0.9992812	0.9999986
179:Psi C to D	0.443E-03	0.620E-03	0.2852E-04	0.0068539
180:Psi C to D	0.801E-03	0.797E-03	0.1137E-03	0.0056224
181:Psi C to D	0.0017389	0.0012505	0.4242E-03	0.0070982
182:Psi C to D	0.0045252	0.0026388	0.0014399	0.0141276
183:Psi C to D	0.0140536	0.0077861	0.0047158	0.0411172
184:Psi C to D	0.0509675	0.0279118	0.0170355	0.1426764
185:Psi C to D	0.1955784	0.0913157	0.0723069	0.4313016
186:Psi C to D	0.5694378	0.1376870	0.3055224	0.7990315
187:Psi C to D	0.8963121	0.0510913	0.7463820	0.9621084
188:Psi C to D	0.9854839	0.0087842	0.9532179	0.9955985
189:Psi C to D	0.9984415	0.0012693	0.9923373	0.9996846
190:Psi C to D	0.9998624	0.159E-03	0.9986725	0.9999857
191:Psi C to D	0.9999899	0.163E-04	0.9997598	0.9999996
192:Psi C to D	0.0018461	0.0018082	0.270E-03	0.0124992
193:Psi C to D	0.0040008	0.0025851	0.0011250	0.0141234
194:Psi C to D	0.0103738	0.0045232	0.0044006	0.0242570
195:Psi C to D	0.0318236	0.0112357	0.0158290	0.0629464
196:Psi C to D	0.1101962	0.0358493	0.0570364	0.2022744
197:Psi C to D	0.3592445	0.0855858	0.2129240	0.5374546
198:Psi C to D	0.7530740	0.0682237	0.5977212	0.8622578
199:Psi C to D	0.9522305	0.0179969	0.9017620	0.9774207
200:Psi C to D	0.9936529	0.0033590	0.9821808	0.9977561

Table 21 Continued

Parameter	Estimate	Standard Error	95% Confidence Interval Lower	Upper
201:Psi C to D	0.9993236	0.541E-03	0.9967576	0.9998592
202:Psi C to D	0.9999403	0.706E-04	0.9993928	0.9999941
203:Psi C to D	0.9999956	0.730E-05	0.9998849	0.9999998
204:Psi C to D	0.0066636	0.0042224	0.0019178	0.0228847
205:Psi C to D	0.0172051	0.0063810	0.0082862	0.0353815
206:Psi C to D	0.0520375	0.0116657	0.0333796	0.0802584
207:Psi C to D	0.1713793	0.0296699	0.1207457	0.2375101
208:Psi C to D	0.4835585	0.0545107	0.3790420	0.5895334

Table 22. Multiple-Sight Transitions Probabilities from A to B and A to C, 2000.

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:S A:South	1.0000000	0.0000000	1.0000000	1.0000000
2:p A:South	1.0000000	0.0000000	1.0000000	1.0000000
3:Psi B to A	0.0000000	0.0000000	0.0000000	0.0000000
4:Psi A to B	0.0035139	0.0013631	0.0016415	0.0075061
5:Psi A to B	0.0073857	0.0019004	0.0044567	0.0122160
6:Psi A to B	0.0144667	0.0024427	0.0103831	0.0201237
7:Psi A to B	0.0263622	0.0033676	0.0205070	0.0338313
8:Psi A to B	0.0446116	0.0053898	0.0351625	0.0564515
9:Psi A to B	0.0700205	0.0084683	0.0551346	0.0885488
10:Psi A to B	0.1019389	0.0120107	0.0806899	0.1280044
11:Psi A to B	0.1379297	0.0168755	0.1080550	0.1744485
12:Psi A to B	0.1741409	0.0268909	0.1275226	0.2332456
13:Psi A to B	0.2062362	0.0454092	0.1310799	0.3091527
14:Psi A to B	0.2303730	0.0725359	0.1183589	0.4002679
15:Psi A to B	0.2438130	0.1064781	0.0941619	0.5000177
16:Psi A to B	0.0000000	0.0000000	0.0000000	0.0000000
17:Psi A to B	0.0000000	0.0000000	0.0000000	0.0000000
18:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000
19:Psi A to C	0.0701546	0.0076460	0.0565697	0.0867021
20:Psi A to C	0.1290086	0.0079990	0.1141251	0.1455143
21:Psi A to C	0.2042240	0.0093453	0.1865163	0.2231517
22:Psi A to C	0.2818389	0.0127977	0.2574462	0.3075855
23:Psi A to C	0.3462584	0.0158940	0.3157987	0.3780327
24:Psi A to C	0.3868420	0.0185851	0.3511064	0.4238390
25:Psi A to C	0.3987690	0.0238645	0.3530427	0.4463319
26:Psi A to C	0.3809547	0.0339828	0.3169263	0.4494080
27:Psi A to C	0.3350771	0.0475175	0.2491170	0.4335717
28:Psi A to C	0.2669734	0.0597100	0.1668592	0.3984293
29:Psi A to C	0.1885183	0.0639695	0.0928555	0.3452292
30:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000
31:Psi A to C	0.0000000	0.0000000	0.0000000	0.0000000

Table 23. Multiple-Sight Transitions Probabilities from B to D and C to D, 2000.

			95% Confidence Interval	
Parameter	Estimate	Standard Error	Lower	Upper
1:S B:BB	1.0000000	0.0000000	1.0000000	1.0000000
2:p D:North	1.0000000	0.0000000	1.0000000	1.0000000
3:Psi D to B	0.0000000	0.0000000	0.0000000	0.0000000
4:p B:BB	0.0000000	0.0000000	0.0000000	0.0000000
5:p B:BB	0.1111105	0.1047560	0.0153928	0.4998616
6:p B:BB	0.2727272	0.1342815	0.0904828	0.5856704
7:p B:BB	0.2142857	0.1096643	0.0707051	0.4943358
8:p B:BB	0.5066097	0.1226048	0.2819218	0.7286591
9:p B:BB	0.4826051	0.1000343	0.2984212	0.6716400
10:p B:BB	0.7244658	0.0718127	0.5650299	0.8418216
11:p B:BB	0.6900445	0.0734593	0.5317458	0.8135888
12:p B:BB	0.7333332	0.0807371	0.5504265	0.8606628
13:p B:BB	1.0000000	0.0000000	1.0000000	1.0000000
14:p B:BB	1.0000000	0.0000000	1.0000000	1.0000000
15:p B:BB	0.0000000	0.0000000	0.0000000	0.0000000
16:p B:BB	0.0000000	0.0000000	0.0000000	0.0000000
17:p B:BB	0.0000000	0.0000000	0.0000000	0.0000000
18:p C:PQ	0.0000000	0.0000000	0.0000000	0.0000000
19:p C:PQ	1.0000000	0.0000000	1.0000000	1.0000000
20:p C:PQ	1.0000000	0.0000000	1.0000000	1.0000000
21:p C:PQ	0.8972603	0.0251277	0.8365650	0.9371095
22:p C:PQ	0.7908068	0.0279441	0.7308067	0.8403550
23:p C:PQ	0.8462427	0.0225893	0.7965967	0.8855128
24:p C:PQ	0.8299265	0.0242125	0.7771076	0.8722859
25:p C:PQ	0.9206005	0.0203909	0.8703173	0.9524521
26:p C:PQ	0.9056605	0.0401505	0.7926057	0.9601828
27:p C:PQ	0.5384619	0.1382623	0.2816530	0.7763604
28:p C:PQ	0.9333334	0.0644058	0.6480034	0.9906949
29:p C:PQ	1.0000000	0.0000000	1.0000000	1.0000000
30:p C:PQ	0.0000000	0.0000000	0.0000000	0.0000000
31:p C:PQ	0.0000000	0.0000000	0.0000000	0.0000000
32:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
33:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
34:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
35:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
36:Psi B to C	0.1878565	0.0821892	0.0744767	0.3993618
37:Psi B to C	0.1427766	0.0650123	0.0555386	0.3205386
38:Psi B to C	0.0248283	0.0244161	0.0035151	0.1552383
39:Psi B to C	0.1426296	0.0417642	0.0784921	0.2452285
40:Psi B to C	0.0836084	0.0388863	0.0326389	0.1978904
41:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
42:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
43:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
44:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
45:Psi B to C	0.0000000	0.0000000	0.0000000	0.0000000
46:Psi B to D	0.0638400	0.0646908	0.0081064	0.3626580
47:Psi B to D	0.1004327	0.0685717	0.0246013	0.3307475
48:Psi B to D	0.1615647	0.0779274	0.0587362	0.3730634
49:Psi B to D	0.2596049	0.1063844	0.1059454	0.5091981

Table 23 Continued.

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
50:Psi B to D	0.4021294	0.1518134	0.1632508	0.6986834
51:Psi B to D	0.5763084	0.1779221	0.2459118	0.8501542
52:Psi B to D	0.7435856	0.1539844	0.3732655	0.9338636
53:Psi B to D	0.8669845	0.0990857	0.5474841	0.9723099
54:Psi B to D	0.9391884	0.0507943	0.7298962	0.9887978
55:Psi B to D	0.9747346	0.0225551	0.8650209	0.9957128
56:Psi B to D	0.9902534	0.0093407	0.9384390	0.9985254
57:Psi B to D	0.9964673	0.0038004	0.9714231	0.9995729
58:Psi B to D	0.9987902	0.0015442	0.9853899	0.9999011
59:Psi B to D	0.9996076	0.616E-03	0.9915098	0.9999820
60:Psi B to D	0.0612414	0.0462856	0.0132853	0.2401695
61:Psi B to D	0.1012019	0.0479155	0.0385525	0.2402221
62:Psi B to D	0.1700416	0.0544732	0.0877146	0.3038988
63:Psi B to D	0.2821323	0.0807890	0.1524210	0.4620528
64:Psi B to D	0.4428331	0.1185161	0.2366481	0.6707990
65:Psi B to D	0.6288718	0.1305889	0.3614005	0.8353531
66:Psi B to D	0.7920367	0.1017722	0.5315135	0.9274573
67:Psi B to D	0.9002430	0.0594912	0.7112653	0.9706398
68:Psi B to D	0.9575244	0.0291216	0.8470982	0.9892157
69:Psi B to D	0.9834345	0.0132161	0.9236976	0.9965769
70:Psi B to D	0.9939694	0.0058620	0.9603845	0.9991084
71:Psi B to D	0.9979314	0.0025409	0.9773875	0.9998143
72:Psi B to D	0.9993286	0.0010539	0.9856069	0.9999691
73:Psi B to D	0.0636864	0.0348026	0.0212086	0.1759476
74:Psi B to D	0.1101343	0.0349223	0.0579880	0.1992548
75:Psi B to D	0.1918634	0.0406875	0.1243055	0.2842210
76:Psi B to D	0.3243812	0.0654339	0.2110004	0.4629397
77:Psi B to D	0.5058353	0.0925425	0.3313048	0.6789551
78:Psi B to D	0.6970329	0.0916250	0.4957032	0.8433813
79:Psi B to D	0.8449971	0.0647931	0.6739918	0.9349589
80:Psi B to D	0.9315907	0.0368799	0.8141409	0.9769242
81:Psi B to D	0.9728722	0.0189131	0.8979918	0.9932018
82:Psi B to D	0.9900562	0.0091399	0.9416499	0.9983747
83:Psi B to D	0.9965802	0.0041566	0.9638845	0.9996858
84:Psi B to D	0.9988891	0.0017630	0.9755741	0.9999506
85:Psi B to D	0.0717484	0.0279317	0.0328582	0.1495507
86:Psi B to D	0.1291254	0.0283477	0.0829591	0.1955057
87:Psi B to D	0.2306798	0.0362717	0.1672738	0.3091962
88:Psi B to D	0.3899733	0.0581779	0.2835845	0.5079746
89:Psi B to D	0.5896314	0.0738994	0.4412315	0.7233318
90:Psi B to D	0.7729637	0.0666411	0.6179438	0.8775483
91:Psi B to D	0.8947888	0.0462157	0.7646641	0.9570086
92:Psi B to D	0.9572595	0.0270917	0.8594928	0.9879524
93:Psi B to D	0.9841725	0.0140865	0.9135357	0.9972749
94:Psi B to D	0.9945354	0.0066262	0.9434421	0.9994966
95:Psi B to D	0.9982225	0.0028494	0.9602003	0.9999235
96:Psi B to D	0.0873675	0.0248221	0.0494360	0.1498164
97:Psi B to D	0.1621969	0.0279667	0.1145230	0.2246809
98:Psi B to D	0.2921593	0.0387092	0.2223900	0.3733088
99:Psi B to D	0.4812454	0.0561485	0.3738165	0.5904367

Table 23 Continued.

			95% Confidence Interval	
Parameter	Estimate	Standard Error	Lower	Upper
100:Psi B to D	0.6873216	0.0648381	0.5489178	0.7988231
101:Psi B to D	0.8459420	0.0560178	0.7027956	0.9272772
103:Psi B to D	0.9756971	0.0209116	0.8769714	0.9955970
104:Psi B to D	0.9915616	0.0101299	0.9163360	0.9992074
105:Psi B to D	0.9972496	0.0044096	0.9394728	0.9998819
106:Psi B to D	0.1144373	0.0253914	0.0732857	0.1743491
107:Psi B to D	0.2159977	0.0315170	0.1605788	0.2840701
108:Psi B to D	0.3824226	0.0422875	0.3035988	0.4679596
109:Psi B to D	0.5946935	0.0575762	0.4788157	0.7009012
110:Psi B to D	0.7856494	0.0625712	0.6389140	0.8836174
111:Psi B to D	0.9061245	0.0488527	0.7579649	0.9674806
112:Psi B to D	0.9640263	0.0292956	0.8365284	0.9929247
113:Psi B to D	0.9874111	0.0146918	0.8855129	0.9987443
114:Psi B to D	0.9958851	0.0064973	0.9154012	0.9998153
115:Psi B to D	0.1597489	0.0296065	0.1098369	0.2265690
116:Psi B to D	0.2993844	0.0349332	0.2356537	0.3719630
117:Psi B to D	0.5031123	0.0449674	0.4157832	0.5902520
118:Psi B to D	0.7166581	0.0612270	0.5834517	0.8203808
119:Psi B to D	0.8694670	0.0576725	0.7110055	0.9474613
120:Psi B to D	0.9486988	0.0381817	0.7989482	0.9885134
121:Psi B to D	0.9818598	0.0200739	0.8559831	0.9979753
122:Psi B to D	0.9940481	0.0090823	0.8918053	0.9997046
123:Psi B to D	0.2336324	0.0383198	0.1669512	0.3168177
124:Psi B to D	0.4194011	0.0385740	0.3462146	0.4963140
125:Psi B to D	0.6434254	0.0520851	0.5362620	0.7379271
126:Psi B to D	0.8261484	0.0609252	0.6741818	0.9160603
127:Psi B to D	0.9295434	0.0459140	0.7695234	0.9811788
128:Psi B to D	0.9747569	0.0257336	0.8325503	0.9966767
129:Psi B to D	0.9916771	0.0120195	0.8728160	0.9995168
130:Psi B to D	0.3475915	0.0562896	0.2467248	0.4642786
131:Psi B to D	0.5709803	0.0526837	0.4661312	0.6698235
132:Psi B to D	0.7780194	0.0601555	0.6391019	0.8740062
133:Psi B to D	0.9068094	0.0512645	0.7476803	0.9696545
134:Psi B to D	0.9660794	0.0309827	0.8169955	0.9945264
135:Psi B to D	0.9887489	0.0150611	0.8608537	0.9991996
136:Psi B to D	0.5036781	0.0864362	0.3400696	0.6665026
137:Psi B to D	0.7277074	0.0705763	0.5707507	0.8430540
138:Psi B to D	0.8812317	0.0563160	0.7210194	0.9551596
139:Psi B to D	0.9559796	0.0355869	0.8054358	0.9912987
140:Psi B to D	0.9852962	0.0179647	0.8550074	0.9986885
141:Psi B to D	0.6781218	0.1111252	0.4371575	0.8510694
142:Psi B to D	0.8539941	0.0703868	0.6592273	0.9464804
143:Psi B to D	0.9448107	0.0410596	0.7853030	0.9876734
144:Psi B to D	0.9814210	0.0207685	0.8499882	0.9979735
145:Psi B to D	0.8265943	0.1049606	0.5315662	0.9524351
146:Psi B to D	0.9331191	0.0518212	0.7326493	0.9861173
147:Psi B to D	0.9772987	0.0242318	0.8350192	0.9972765
148:Psi B to D	0.9216004	0.0730578	0.6183295	0.9884119
149:Psi B to D	0.9731702	0.0300359	0.7918868	0.9971162
150:Psi B to D	0.9693202	0.0399606	0.6940829	0.9977323

Table 23 Continued.

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
151:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
152:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
153:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
154:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
155:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
156:Psi C to B	0.0095344	0.0071609	0.0021729	0.0408158
157:Psi C to B	0.0150341	0.0073809	0.0057133	0.0389649
158:Psi C to B	0.0039002	0.0038357	0.565E-03	0.0263991
159:Psi C to B	0.0482131	0.0190365	0.0219713	0.1025120
160:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
161:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
162:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
163:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
164:Psi C to B	0.0000000	0.0000000	0.0000000	0.0000000
165:Psi C to D	0.0015584	0.0011847	0.350E-03	0.0068940
166:Psi C to D	0.0046242	0.0025555	0.0015623	0.0136050
167:Psi C to D	0.0133286	0.0057103	0.0057346	0.0306687
168:Psi C to D	0.0369573	0.0143048	0.0171562	0.0778032
169:Psi C to D	0.0962539	0.0369693	0.0442545	0.1967735
170:Psi C to D	0.2240714	0.0799714	0.1049279	0.4156732
171:Psi C to D	0.4334114	0.1184391	0.2291220	0.6631543
172:Psi C to D	0.6643835	0.1079596	0.4338684	0.8364251
173:Psi C to D	0.8334689	0.0651072	0.6661944	0.9262050
174:Psi C to D	0.9251607	0.0313453	0.8357996	0.9677654
175:Psi C to D	0.9675643	0.0146227	0.9228910	0.9867282
176:Psi C to D	0.9859794	0.0075313	0.9602775	0.9951355
177:Psi C to D	0.9938637	0.0042988	0.9760098	0.9984515
178:Psi C to D	0.9972635	0.0025635	0.9829963	0.9995649
179:Psi C to D	0.0047127	0.0026406	0.0015683	0.0140724
180:Psi C to D	0.0135816	0.0051751	0.0064162	0.0285192
181:Psi C to D	0.0376415	0.0105162	0.0216624	0.0646289
182:Psi C to D	0.0979243	0.0242678	0.0595824	0.1568250
183:Psi C to D	0.2274017	0.0522967	0.1410662	0.3453327
184:Psi C to D	0.4380964	0.0785771	0.2943134	0.5930874
185:Psi C to D	0.6686190	0.0721287	0.5159673	0.7924899
186:Psi C to D	0.8360969	0.0441787	0.7305869	0.9056239
187:Psi C to D	0.9264694	0.0227218	0.8676051	0.9603578
188:Psi C to D	0.9681570	0.0121704	0.9334432	0.9850551
189:Psi C to D	0.9862404	0.0071559	0.9622619	0.9950613
190:Psi C to D	0.9939788	0.0043599	0.9753646	0.9985493
191:Psi C to D	0.9973150	0.0026493	0.9816250	0.9996129
192:Psi C to D	0.0128081	0.0050076	0.0059345	0.0274235
193:Psi C to D	0.0355473	0.0085638	0.0220901	0.0567271
194:Psi C to D	0.0927997	0.0149914	0.0672990	0.1266510
195:Psi C to D	0.2171322	0.0297276	0.1644852	0.2809635
196:Psi C to D	0.4235279	0.0471160	0.3348021	0.5174752
197:Psi C to D	0.6553249	0.0464688	0.5595414	0.7399593
198:Psi C to D	0.8277911	0.0315246	0.7570571	0.8811633
199:Psi C to D	0.9223178	0.0192883	0.8750767	0.9526606
200:Psi C to D	0.9662734	0.0122351	0.9320939	0.9835528

Table 23 Continued.

			95% Confidence Interval	
Parameter	Estimate	Standard Error	Lower	Upper
201:Psi C to D	0.9854103	0.0078043	0.9588604	0.9949168
202:Psi C to D	0.9936126	0.0048601	0.9719710	0.9985690
203:Psi C to D	0.9971511	0.0029541	0.9785383	0.9996280
204:Psi C to D	0.0311111	0.0078936	0.0188568	0.0509159
205:Psi C to D	0.0818248	0.0111441	0.0624714	0.1064928
206:Psi C to D	0.1946075	0.0158213	0.1654542	0.2274973
207:Psi C to D	0.3902657	0.0253590	0.3418477	0.4409469
208:Psi C to D	0.6235494	0.0298308	0.5635443	0.6799894
209:Psi C to D	0.8072384	0.0258686	0.7514429	0.8529598
210:Psi C to D	0.9118451	0.0199042	0.8642501	0.9438374
211:Psi C to D	0.9614791	0.0141079	0.9220607	0.9813643
212:Psi C to D	0.9832894	0.0092852	0.9510740	0.9944170
213:Psi C to D	0.9926751	0.0058023	0.9659437	0.9984581
214:Psi C to D	0.9967313	0.0035130	0.9735765	0.9996039
215:Psi C to D	0.0669716	0.0102514	0.0494668	0.0900836
216:Psi C to D	0.1629140	0.0121847	0.1404175	0.1882255
217:Psi C to D	0.3401659	0.0155528	0.3103749	0.3712769
218:Psi C to D	0.5715754	0.0219226	0.5281733	0.6139036
219:Psi C to D	0.7713245	0.0253725	0.7178581	0.8172385
220:Psi C to D	0.8928335	0.0231083	0.8384381	0.9304343
221:Psi C to D	0.9526154	0.0174146	0.9041968	0.9771809
222:Psi C to D	0.9793363	0.0116702	0.9386698	0.9932323
223:Psi C to D	0.9909219	0.0073208	0.9567981	0.9981447
224:Psi C to D	0.9959449	0.0044299	0.9662298	0.9995259
225:Psi C to D	0.1265807	0.0123160	0.1043427	0.1527499
226:Psi C to D	0.2774019	0.0155507	0.2479753	0.3088863
227:Psi C to D	0.4983628	0.0199424	0.4593651	0.5373804
228:Psi C to D	0.7152407	0.0261727	0.6613029	0.7636586
229:Psi C to D	0.8611871	0.0272503	0.7987337	0.9065290
230:Psi C to D	0.9373846	0.0220107	0.8777266	0.9689643
231:Psi C to D	0.9724460	0.0152248	0.9205611	0.9907820
232:Psi C to D	0.9878468	0.0096895	0.9435362	0.9974772
233:Psi C to D	0.9945620	0.0059035	0.9556159	0.9993567
234:Psi C to D	0.2090456	0.0176040	0.1766275	0.2456386
235:Psi C to D	0.4061628	0.0209198	0.3658992	0.4477286
236:Psi C to D	0.6335954	0.0248170	0.5837408	0.6807447
237:Psi C to D	0.8102881	0.0301793	0.7440426	0.8625555
238:Psi C to D	0.9115558	0.0275519	0.8406357	0.9526912
239:Psi C to D	0.9604701	0.0203224	0.8948489	0.9857897
240:Psi C to D	0.9824438	0.0133653	0.9245510	0.9961021
241:Psi C to D	0.9921206	0.0082872	0.9403512	0.9990066
242:Psi C to D	0.3033016	0.0264793	0.2540300	0.3575494
243:Psi C to D	0.5239564	0.0244952	0.4758724	0.5716002
244:Psi C to D	0.7310801	0.0293462	0.6698588	0.7845992
245:Psi C to D	0.8677267	0.0327726	0.7894084	0.9198751
246:Psi C to D	0.9392658	0.0272228	0.8585449	0.9752514
247:Psi C to D	0.9726913	0.0190375	0.8973516	0.9931565
248:Psi C to D	0.9876762	0.0121992	0.9182969	0.9982532
249:Psi C to D	0.3930890	0.0363815	0.3244835	0.4661894
250:Psi C to D	0.6153517	0.0292448	0.5566794	0.6708502

Table 23 Continued.

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
251:Psi C to D	0.7942542	0.0354059	0.7162839	0.8551306
252:Psi C to D	0.9009965	0.0355275	0.8065449	0.9520737
253:Psi C to D	0.9544627	0.0275947	0.8579330	0.9864404
254:Psi C to D	0.9792365	0.0186960	0.8860808	0.9965151
255:Psi C to D	0.4653427	0.0481625	0.3732571	0.5598529
256:Psi C to D	0.6774430	0.0396973	0.5953131	0.7499072
257:Psi C to D	0.8319667	0.0440240	0.7275851	0.9017529
258:Psi C to D	0.9193762	0.0398296	0.7991056	0.9703182
259:Psi C to D	0.9624880	0.0294845	0.8381132	0.9921974
260:Psi C to D	0.5137110	0.0649356	0.3882627	0.6374553
261:Psi C to D	0.7134996	0.0568004	0.5909341	0.8110820
262:Psi C to D	0.8515378	0.0563174	0.7054909	0.9321278
263:Psi C to D	0.9280872	0.0470266	0.7643426	0.9808986
264:Psi C to D	0.5366300	0.0891315	0.3645248	0.7004295
265:Psi C to D	0.7273174	0.0812814	0.5443275	0.8562309
266:Psi C to D	0.8571739	0.0744694	0.6456081	0.9518569
267:Psi C to D	0.5341775	0.1221329	0.3046836	0.7500615
268:Psi C to D	0.7206890	0.1158272	0.4551424	0.8885166
269:Psi C to D..	0.5063196	0.1641481...	0.2206561	0.7879156

Appendix F.

Adjusted Arrivals and Departures and Mean Lengths of Stay

Adjusted arrival and departure dates for multiple-sight data correct for the assumption $p_i^A = 1$ and $p_i^D = 1$ (Tables 24 and 25).

Table 24. Estimated arrival times if first observed in period *i*.

Period *i*	1999				2000			
	B		C		B		C	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
1	1.0	0.0	1.0	0.0	1.0	0.0	1.0	0.0
2	1.5	0.5	1.5	0.5	2.0	0.0	2.0	0.0
3	2.0	0.8	2.0	0.8	2.5	0.5	2.5	0.5
4	3.1	0.9	3.1	0.9	3.1	0.8	4.0	0.0
5	4.0	1.0	3.9	1.1	3.9	1.1	5.0	0.0
6	4.9	1.1	5.1	1.1	4.7	1.3	5.6	0.2
7	5.9	1.2	6.1	1.0	6.0	1.4	6.9	0.3
8	6.5	1.4	7.3	0.8	7.2	1.4	7.9	0.3
9	8.1	1.1	8.4	0.6	8.6	1.0	8.9	0.3
10	8.7	1.3	9.4	0.6	9.7	0.8	9.9	0.2
11	10.3	0.9	10.4	0.6	10.8	0.6	10.9	0.2
12	11.2	0.8	11.5	0.5	12.0	0.0	11.7	0.5
13	12.5	0.5	12.0	0.8	13.0	0.0	12.9	0.3
14	14.0	0.0	12.5	1.1	13.5	0.5	14.0	0.0
15	15.0	0.0	13.0	1.4	14.0	0.8	14.5	0.5

Table 25. Estimated departure times if last observed in period *i*.

Period *i*	1999				2000			
	B		C		B		C	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
1	1.9	1.1	1.9	1.0	2.8	1.6	1.5	0.5
2	2.4	0.9	2.4	0.8	3.3	1.4	2.0	0.0
3	3.7	1.1	3.5	0.8	4.0	1.2	3.0	0.0
4	4.7	1.1	4.3	0.6	4.8	0.9	4.1	0.3
5	5.7	1.0	5.2	0.5	5.5	0.8	5.1	0.4
6	6.7	0.8	6.1	0.3	6.4	0.7	6.1	0.3
7	7.3	0.6	7.1	0.2	7.2	0.5	7.1	0.3
8	8.6	0.6	8.1	0.2	8.2	0.5	8.0	0.2
9	9.1	0.4	9.1	0.2	9.1	0.3	9.1	0.3
10	10.2	0.4	10.0	0.0	10.0	0.0	102	0.5
11	11.0	0.1	11.0	0.0	11.0	0.0	11.0	0.2
12	12.0	0.0	12.0	0.0	12.0	0.0	12.0	0.0
13	13.0	0.0	13.0	0.0	13.0	0.0	13.0	0.0
14	14.0	0.0	14.0	0.0	14.0	0.0	14.0	0.0
15	15.0	0.0	15.0	0.0	15.0	0.0	15.0	0.0

Table 26. Mean length of stay (T) and associated standard error (SE) estimated in weeks for each cohort, year and stratum (S).

			Cohort													
Year	**S**		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
	\	**T**	3.7	3.6	4.4	4.2	3.9	3.5	3.0	2.7	2.4	2.0	1.6	1.3	1.3	1.1
	B		2	6	9	7	3	0	2	1	6	8	9	9	9	9
		S	2.3	2.4	2.0	1.8	1.6	1.5	1.5	1.3	1.1	0.9	0.7	0.6	0.5	0.4
1999		**E**	5	6	2	3	8	7	1	6	4	6	8	0	9	2
		T	4.2	4.0	3.7	3.2	2.7	2.6	2.5	2.0	1.8	1.6	1.3	1.1	1.0	1.0
	C		9	6	1	6	3	8	2	6	7	5	7	8	8	3
		S	1.6	1.4	1.4	1.4	1.4	1.3	1.1	1.0	0.9	0.7	0.5	0.4	0.2	0.1
		E	0	8	1	1	7	2	2	6	2	5	8	1	8	7
		T	9.6	7.9	6.4	5.0	3.9	3.1	2.5	2.1	1.8	1.6	1.5	1.4	1.4	1.4
	B		4	5	2	9	9	7	4	0	1	2	1	5	4	4
		S	1.0	1.1	1.1	1.1	1.0	0.9	0.8	0.7	0.6	0.6	0.5	0.5	0.5	0.5
2000		**E**	8	2	5	4	9	7	7	7	9	2	8	5	3	0
		T	6.9	5.9	4.9	4.1	3.4	2.8	2.4	2.0	1.8	1.7	1.6	1.6	1.5	1.4
	C		2	1	9	7	6	6	1	8	2	4	5	1	9	9
		S	1.4	1.4	1.3	1.3	1.2	1.1	1.0	0.9	0.8	0.8	0.7	0.7	0.7	0.5
		E	4	1	8	3	5	6	5	5	8	2	7	5	1	0

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